WEST GULF COASTAL PLAIN ECOREGIONS

Michael H. MacRoberts and Barbara R. MacRoberts

Bog Research
740 Columbia
Shreveport, LA 71104, U.S.A.
and
Herbarium, Museum of Life Sciences
Louisiana State University-Shreveport
Shreveport, LA 71115, U.S.A.

ABSTRACT

We review the literature on West Gulf Coastal Plain ecoregions and examine the methodology used by ecoregion mappers. Ecoregion mapping has been done almost entirely without quantitative assessment. We suggest that quantitative descriptions should replace impressionistic descriptions.

KEY WORDS: West Gulf Coastal Plain, Ecoregions

RESUMEN

Hemos revisado la bibliografía de las ecorregiones de la West Gulf Coastal Plain y examinado la metodología usada por los cartógrafos de ecorregiones. La cartografía ecorregional ha sido realizada casi totalmente sin evaluación cuantitativa. Sugerimos que las descripciones cuantitativas deben reemplazar a las descripciones impresionistas.

INTRODUCTION

Half a century ago, Webb (1950) examined the methodology of biogeographers who had mapped Texas and Oklahoma ecoregions. He found not only that ecoregional mappers did not agree among themselves but that ecoregional mapping was subjective. He suggested a remedy: "quantitative methods must be developed before general agreement on the extent of the major [ecoregions] can be reached. As long as personal opinion and individual judgment are the only basis for judging the extent of the [ecoregions], fundamental and insoluble differences of opinion will continue" (Webb 1950:246). Using vertebrates, he quantitatively assessed the ecoregions of Texas and Oklahoma. His ecoregions did not correspond with those developed by botanists and botanically oriented ecologists. A decade and a half later, Gleason and Cronquist (1964:177), referring to the entire North American continent, reiterated Webb's point in almost the same words but made no quantitative analysis. More recently, Hargrove and Luxmoore (1998), again looking at the entirety of North America, recognized the same thing: "Because the delineation [of ecoregions] is based on subjective criteria, there are as many sets of ecoregions as there are experts."

These assertions prompted us to examine the history of floristic ecoregion delineation in the West Gulf Coastal Plain (WGCP). We will be concerned

mainly with three ecoregions: Longleaf Pine (LLP), Post Oak Savanna (POSa), and Oak-Pine-Hickory (OPH). One of the traditional designations and locations of these WGCP ecoregions is given in Figure 1.

There are numerous descriptions of each of these ecoregions (e.g., Tharp 1939; Gould 1962; Correll & Johnston 1970; LBJ School of Public Affairs 1978; Hatch et al. 1990; Telfair 1999). The lack of pines, the codominance of oaks and hickories, and the ubiquitous presence of *Quercus stellata* Wang. are always emphasized when the POSa region is described, the combination of pines, oaks, and hickories is emphasized in the description of the OPH ecoregion, and the LLP ecoregion is defined as being coterminous with the distribution of *Pinus palustris* Mill.

METHODS

1. Ecoregional mappers.—We surveyed the ecoregional literature dealing with the eastern part of the WGCP to see if Webb (1950), Gleason and Cronquist (1964), and Hargrove and Luxmoore (1998) were correct in their assessment of ecoregional mapping. The literature dealing directly or indirectly with the ecoregions of this area is extensive (Cooper 1859; Transeau 1903; Harshberger 1911; Shreve 1917; Shantz & Zon 1924; Tharp 1926, 1939, 1952; Carter 1931; Fenneman 1938; Dice 1943, 1968; Blair 1950; Braun 1950; Turner 1959; Gould 1962; Gleason & Cronquist 1964; Kuchler 1964; Kuchler & McCormick 1965; LBJ School of Public Relations 1978; Bailey 1980; McMahan et al. 1984; Omernik 1986; Takhtajan 1986; Diamond et al. 1987; De Graaf et al 1988; Diamond & Smeins 1988; Greller 1988; Barbour & Christensen 1993; Thorne 1993; Bailey et al. 1994; McNab & Avers 1994; Keys et al. 1995; Weakley et al. 1998; Diggs et al. 1999; Ricketts et al. 1999a, 1999b; Delcourt & Delcourt 2000). Mappers are discussed and their maps reproduced in the Appendix.

2. Floristics.—We made a number of quantitative ecoregional comparisons to see how similar or different these regions are. Since there is no complete floristic survey of any of the WGCP ecoregions, we had to rely on floristic lists from each (e.g., Anon. n.d.; McBryde 1933; Matos & Rudolph 1985; Nixon 1985; Bridges & Orzell 1989; Hatch et al. 1990; Orzell 1990; Louisiana Natural Heritage Program 1998; Turner et al. 1999; Van Kley 1999a, 1999b; MacRoberts & MacRoberts 2001), which we have compared with distributional data given in various floras, atlases, and plant lists (e.g., Smith 1988; MacRoberts 1989; Taylor & Taylor 1989; Hatch et al. 1990; Thomas & Allen 1993-1998; Kartesz & Meacham 1999; Turner 2003) and community classifications (Diamond et al. 1987; Louisiana Natural Heritage Program 1998; Bezanson 2000). To establish the existence of different floristic ecoregions one would expect there to be 1) significant regional floristic differences between ecoregions, 2) significant regional community differences between ecoregions, and 3) higher similarity within different parts of an ecoregion than between ecoregions. We were unable to compare species abundances between regions since the data are not available.

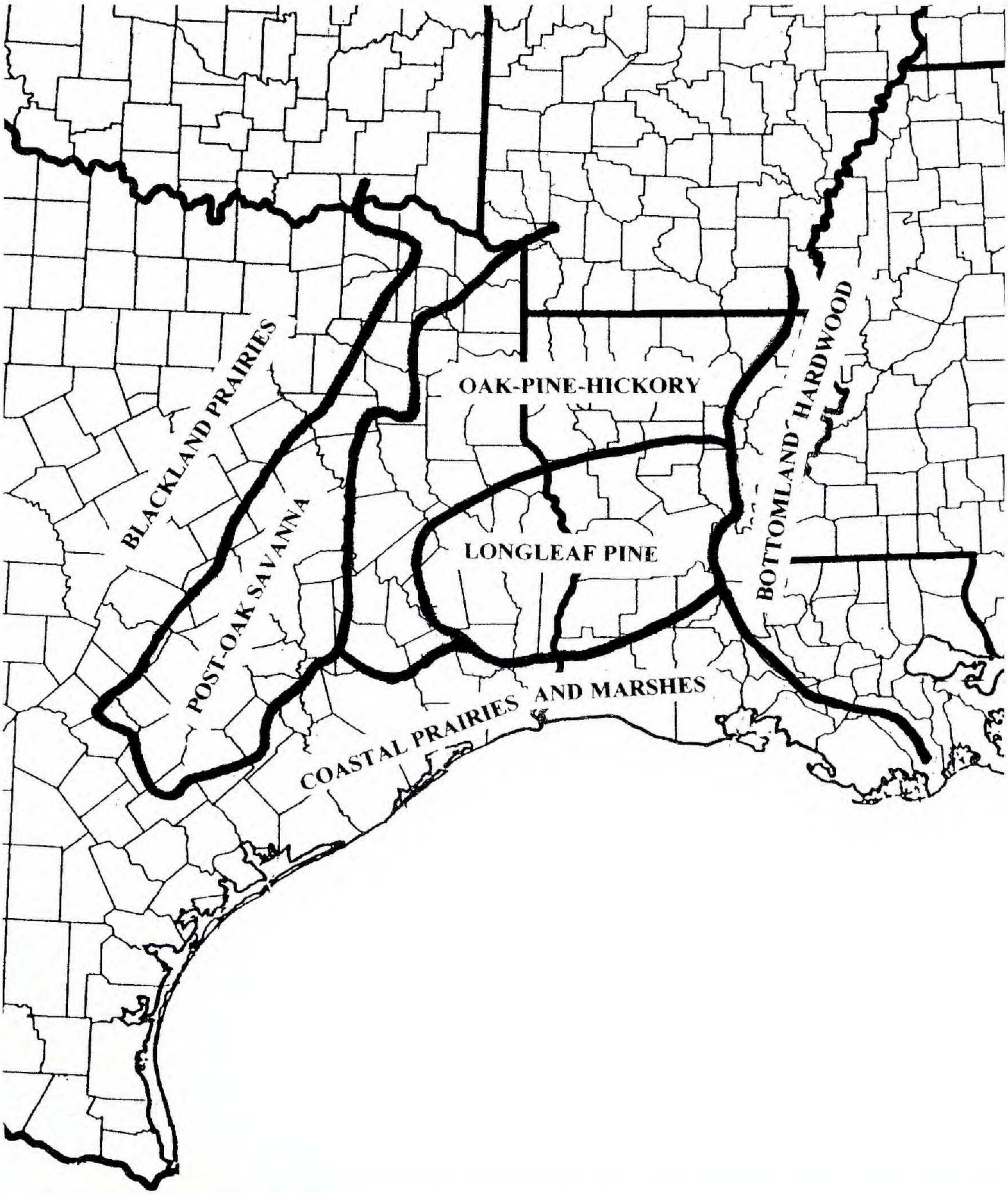

FIG. 1. Standard location of West Gulf Coastal Plains vegetation areas (ecoregions).

3. Soils.—The interrelationship of soils and flora has long fascinated ecologists (Warner 1926). Eastern versus western United States is clearly marked by a soil break (Carter 1931), and in the WGCP many plant communities are correlated directly with soils—e.g., blackland prairies, Weches Formation, and sandstone glades and outcrops. We surveyed the WGCP soil literature (Carter 1931; Godfrey et al. 1973; Steila 1993) to see if soils correlate with floristic ecoregional delineations.

4. Vertebrates.—Although our main focus is on the flora, we examined the literature on ecoregional distribution of vertebrates (except fish) in the WGCP in an attempt to see if animal distributions correlate with traditional plant ecoregions (Blair 1950; Webb 1950; McCarley 1959; Neck 1986; Gehlbach 1991; Wilkins 1992; Ward et al. 1994). Also, using lists of birds, reptiles, amphibians, and mammals from the WGCP, we plotted vertebrate distribution to see if there were any correlations with ecoregion.

RESULTS

1. Ecoregional mappers.—We confirmed the assessment of Webb (1950), Gleason and Cronquist (1964), and Hargrove and Luxmoore (1998). There have been dozens of WGCP ecoregional mappers, but, with one exception, there has been no floristic mapping based on quantitative data. Instead, we found that ecoregional mappers almost invariably base their maps on the presence or absence of one or a few "diagnostic" trees or a "suite" of trees, with little or no attention paid to herbaceous and understory species. None of the modern armament of statistical ecology and sampling (e.g., Mueller-Dombois & Ellenberg 1974; Peet et al. 1998) has been applied although it is beginning to be used in WGCP community ecology (Dale 1986; Turner et al. 1999). We also found little agreement among mappers.

Only Turner (1959) used quantitative methods and, not surprisingly, his results are unique (Fig. 2). Turner's method was relatively simple: he calculated "the percentage of species restricted to a given region ('endemic' species) and the percentage of species shared with other provinces ('shared' species). The percentage of restriction, expressed as that fraction of the total species known to occur in the province under consideration, was taken as the naturalness of the floral region" (Turner 1959:5 [see also Webb 1950 for comparable method using vertebrates]). He discovered that there were basically five regions in Texas that fit his criterion of 40% or higher for "endemism." Interestingly, he also found that attempts to delineate clearly distinct, but smaller, subdivisions resulted in such heterogeneous figures that these regions, on a floristic basis, would not be strictly comparable. Turner found that floristically the POSa, LLP, OPH, and Cross Timbers are similar and, therefore, he lumped them (his Appalachian) and separated from them the Prairie (his Campestrian) and South Texas Plains (his Tamaulipan) because they are different. This is a singular result among biogeographers, who invariably divide the WGCP into many ecoregions.

2. Floristics.—Using floristic and plant community lists from various areas within the POSa, OPH, and LLP regions, we compared floristic and community similarities and differences throughout the LLP, POSa, and OPH region of the WGCP. The result: all regions had greater than 90% of their flora in common. Virtually the same holds for communities. For example, pockets of prairie occur throughout the OPH, POSa, and LLP regions, bogs occur in all three

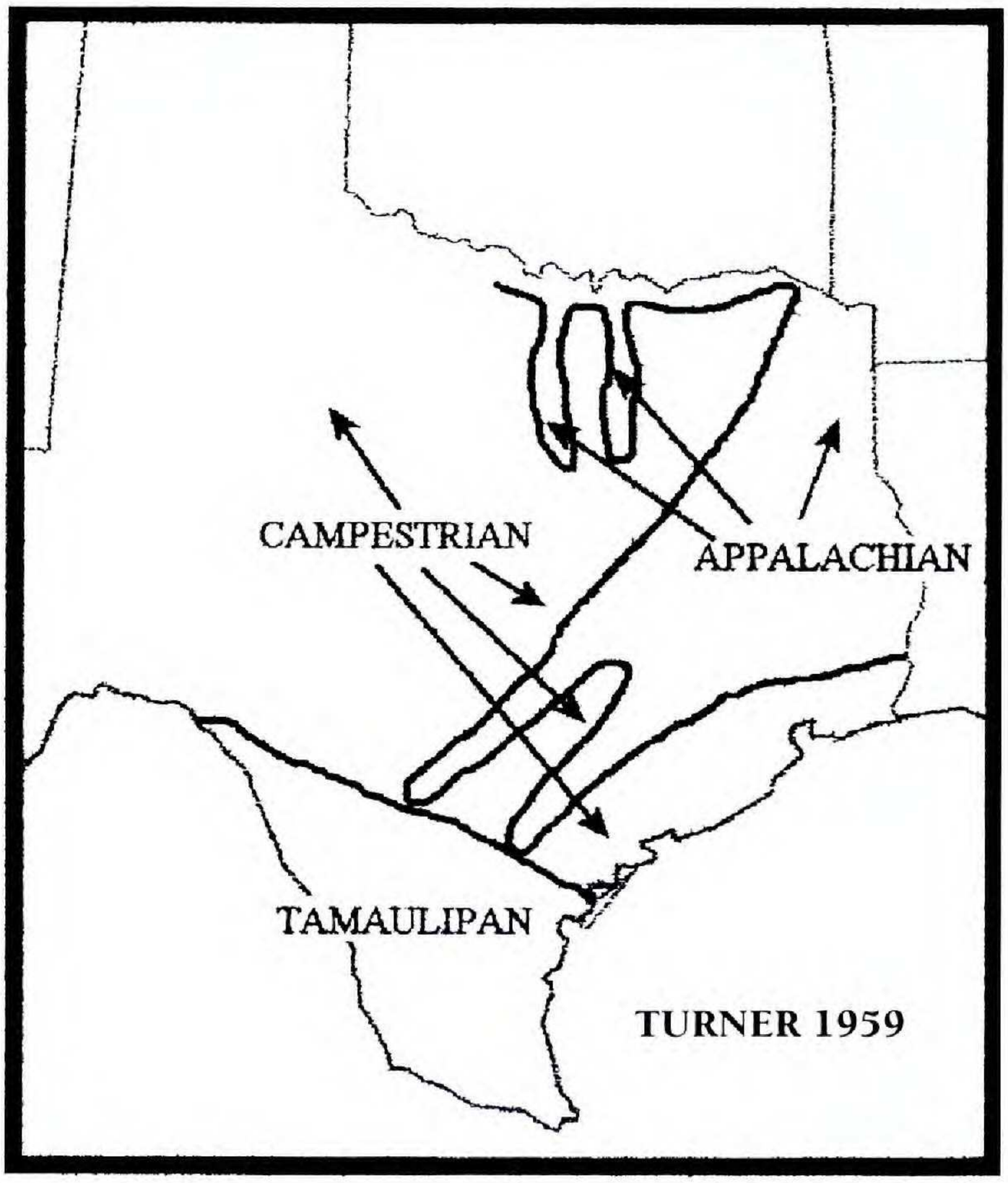

Fig. 2. B.L. Turner's (1959) Texas vegetation areas.

regions, notably in the LLP and POSa areas, hardwood-beech slopes are found in both LLP and OPH regions, baygalls are common in all three regions, grossarenic xeric sandylands and xeric oak woodlands are especially common in the POSa region but present in the other two regions as well, sandstone outcrops or barrens occur in the POSa and LLP regions, and so on. Since no one has collected the data to perform an analysis of species abundance, very little can be said about that parameter.

One of the predictions of biogeography (we assume) would be that different sections of the same ecoregion should be floristically more similar to each other than to different ecoregions. Biogeographers such as Kuchler (1964; see also Gleason & Cronquist 1964; Cronquist 1982; Takhtajan 1986) have placed states as distant as Maine, Michigan, and Texas in the same ecoregion or province (Oak-Hickory Forest, Appalachian Province). We compared the floristics between Kuchler's Oak-Hickory Forest in Texas (POSa ecoregion) and Oak-Hickory Forest in Missouri 300 miles away and the Oak-Hickory-Pine Forest (OPH ecoregion) in Mississippi 300 miles away. We found that the different ecoregions were more similar (Texas POSa and Mississippi OPH: 81% of species

in common) than areas within the "same" ecoregion (Texas POSa and Missouri POSa: 67% of species in common). We also compared the differences between Michigan and North Carolina and the POSa of east central Texas. Michigan and North Carolina are both 1000 miles from east central Texas, but Michigan is supposedly in the same province or ecoregion, while North Carolina is not. The result: Michigan had 44% and North Carolina had 75% of the species in common with Texas.

3. Soils.—A survey of the soil literature uncovered no overall soil/floristic correlations for the LLP, OPH, or the POSa ecoregions but instead a great interdigitation of soil types (largely Alfisols and Ultisols) throughout the region (Tharp 1952; Godfrey et al. 1973; Smeins & Diamond 1986). However, the prairie soils (both blackland and coastal) do fall out clearly along traditional floristic boundaries. On a broader note, Hargrove and Luxmoore (1998), using multivariate analysis of nine edaphic variables (including: elevation, soil, water, temperature, climate), produced a high resolution map of the United States. Overlaying this on traditional WGCP vegetation maps shows no correlations. The LLP, POSa, and OPH regions do not stand out individually but merge together into one general area.

4. Vertebrates.—Zoologists have long known that no correlation exists between vertebrates and the traditional floristic ecoregions. Instead, the prairie areas form a break between eastern and western species. Central Texas is a transition zone for vertebrates, but central Texas begins west of the POSa region (Webb 1950; Neck 1986; Gehlbach 1991; Wilkins 1992; Ward 1994). As far as vertebrates are concerned, the eastern WGCP as a whole is significant, not its components. Our survey of vertebrate distribution confirms the zoologists' contentions.

DISCUSSION

The most obvious finding of this study is that only one WGCP floristic ecoregion map was developed using quantitative methods and, parenthetically, it was subsequently ignored. All other schemes are subjective, the criticism made by Webb (1950), Gleason and Cronquist (1964), and Hargrove and Luxmoore (1998). There are no methodological descriptions, no quantitative data, no demarcation criteria, and no statistical analyses. Apparently, ecoregions are self-evident and impressionistic description is considered sufficient. The question Webb (1950:426) asked five decades ago is as pertinent today as it was then: "How different must the fauna and flora of two areas be before they are recognized as examples of different ecoregions?"

Only Turner (1959) attempted an answer, and he found that the eastern WGCP constituted a single floristic region. We have confirmed this finding: between 90% and 99% of species occurring in the LLP, OPH, and POSa regions also occur in the others, and the majority of plant communities are common to all three regions. When traveling from one region to another, the botanist does

not encounter a new flora, the zoologist a new fauna, and the ecologist a new set of plant and animal communities. What differences exist are not of kind but of degree. Sharp boundaries simply do not exist.

Many individuals have noted an east-west gradient between OPH and POSa regions. Tharp (1926:48) pointed out that *Quercus stellata* and *Q. marilandica* Muenchh. are often codominants with pine in the OPH ecoregion and that the transition to POSa "... merely means the gradual decrease of pine until it has disappeared." McCarley (1959:390) said: "The boundary between the pine-oak region and the oak-hickory region is nowhere sharply marked, but is characterized by a gradual decrease in pine and an increase in oaks and hickories." Wilson (1990:184) said: "At the western edge of the piney woods, the mixed pine-oak forest gave way to ... a hardwood forest similar in composition to the deciduous component of the mixed forest," and further, the pines disappear "from the forest leaving a mixed hardwood forest." Currie (1991), Nesom and Brown (1998) and Nesom et al. (1997) documented the loss of tree species diversity, not just pine, in the WGCP as one moves west. Although pockets of pines occur in the POSa region almost to Austin and Paris, Texas (Warner 1926; Wilson 1989), pines tend to drop out of the flora just before the true prairies are reached. Blair (1950) clearly had trouble separating the OPH and LLP regions from the POSa and spoke of an ecotone between them and the prairies farther west. Recent analysis of the distribution of *Pinus palustris* in east Texas does not support the simple story of savannas dominated by single species but rather tells a complex story involving the occurrence of mixed longleaf-shortleaf pine savannas not only on the periphery of the *Pinus palustris* range, but at its center (Evans 1997). Monk et al. (1990:77), in their study of so-called oak-hickory communities across the eastern United States, found that hickory was seldom, if ever, a dominant or codominant: "No real evidence was found for a regional oak-hickory forest." Dale and Ware (1999), commenting on this matter, pointed out that in contrast to these earlier findings, hickory may be a codominant in certain areas west of the Mississippi River.

Few question how the lines get on ecoregional maps—why a given line forms a polygon without internal polygons of other types. What is evident is that ecoregion delineations leave out all the messy detail; they are idealizations that actually describe very little of the area encircled. For example, at the macro-level the Takhtajan (1986) and Cronquist and Gleason (1964) descriptions of the Texas POSa region (their Appalachian and Eastern Deciduous Forest provinces) are so far out of the range of the "type" that they are simply not the same association of plants. At the micro-level, adjacent areas designated as different are not floristically different at all. As far as we have been able to ascertain, the LLP "ecoregion" is simply an autecological statement about the presettlement distribution of *Pinus palustris*. There is no unique LLP "ecoregion" flora with a substantial number of endemics and unique plant communities. The POSa

"ecoregion" is the western edge of the southeastern pine/oak forest and, as such, many species drop out; notably pines. But again there is no floristic break or large number of endemics or unique communities by which the POSa "ecoregion" can be described. The OPH "ecoregion" is similarly undifferentiated—aside from the absence of *Pinus palustris*, it is difficult to find anything that warrants setting it off as a separate region.

While the construction of ecoregional maps might seem to have little or no import, this is not entirely so. Ecoregions are the basis for deciding conservation priorities. For example, Diamond et al. (1997), Ricketts et al. (1999a, 1999b), Weakley et al. (1999), and Myers et al. (2000) all are concerned with priorities for conservation of rare species, endemic species, and rare habitat, and decisions about them are based on the concentration of rare species, endemics, and so on, which in turn is based on which map is selected: Ricketts et al. (1999a, 1999b) chose Omernick (1986), Weakley et al. (1998) chose Bailey et al. (1994), and Diamond et al. (1997) chose Gould (1962). Setting aside the almost insurmountable problems of how species numbers and their rareness are calculated for these ecoregions, the fact remains that size of area and its location make a lot of difference in deciding whether or not an ecoregion is an ecological "hot spot" or "cold spot." For example, Ricketts et al. (1999a) concluded that the OPH plus LLP ecoregions (their "Piney Woods Forests") had only 7 endemic plants and the POSa region (their "East Central Texas Forests") also had only 7 endemic plants. However, by combining the POSa, OPH, and LLP regions, we calculate that these three "regions" together have approximately 100 endemic or near-endemic plants, not 14!—thereby instantly changing the WGCP from an ecological cold spot to an ecological hot spot. A map that combines the POSa, LLP, and OPH regions makes for very different biogeography and conservation than one that divides them, and the decisions made by conservationists on the basis of one map may be very different from decisions made using another map.

We are not suggesting that the WGCP or that part of it we have examined in this paper is uniform. Quite the contrary. Previous biologists related something they were familiar with and observed, and we, like our predecessors, can see what was being referred to. If we are attentive, we can tell when we have entered the LLP region by the presence of *Pinus palustris*, and traveling west, we also note when pine vanishes and the landscape is dominated by oaks. We can see these changes because we have been conditioned to look for them and because they are there. We also have no doubt that in these different regions there are differences in species abundance. Thus, the absence of pines from the POSa region and the presence of pines in the OPH and LLP regions signals difference in canopy structure. But lacking in any of these ecoregional descriptions is hard data (floristic lists and abundance data) and statistical procedures and operations for determining when two samples are ecoregionally the "same" or "different." Instead, cultural idealizations and stereotypy substitute for concrete description and

analysis. Consequently, even if we wished to provide a brief summary description of any region inorder to recognize its most valuable or "true" features based on previous delineations would be to rely on idealized and stereotyped descriptions, and would be confounded by precisely what we are describing here.

It is premature to make any definitive statement on the WGCP ecoregions. However, on the basis of our experience and limited floristic sampling, we would say that there is certainly no reason to separate the LLP region from the OPH region. There is nothing revolutionary in this since about half of the ecoregion mappers have already lumped them. Our current thinking about the POSa region is that it is virtually identical floristically to the OPH and LLP regions minus some tree species. But even this is difficult to maintain because, in northern Texas, pine is a part of the POSa flora. Areas such as the Gus Engeling Wildlife Management Area (POSa) in Anderson County are identical edaphically and floristically to Woods County (OPH): POSa habitat simply exists in Wood County with pine on it (see Wilson 1990). This is also the case in such areas as the "Lost Pines" near Bastrop. In conclusion, we find Turner's (1959) analysis approximately what we envision.

APPENDIX

This is a survey of the biogeographers who have produced maps of the WGCP; they are reproduced so they can be understood and compared.

The literature describing and illustrating ecoregions was located by tracing bibliographical entries and by consulting Kuchler and McCormick (1965). Vegetation mapping of the WGCP did not begin in earnest until the twentieth century.

Several early botanists described WGCP vegetation but did not give maps. Without maps it is very difficult, if not impossible, to interpret ecoregion locations precisely; therefore, these descriptions are excluded from this review (e.g., Bray 1906; Warner 1926). Some authors present maps but add little to previous descriptions; these are also excluded from the present discussion (e.g., Allred & Mitchell 1955; McMahan et al. 1984). General accounts of early WGCP botanical research and descriptions of vegetation are given by Harper (1920), Tharp (1926), and Geiser (1948).

WGCP ecoregion terminology has never been standardized and any attempt to cross-index all usages would be almost impossible. We have, therefore, taken the liberty of standardizing it for this paper. Since we reproduce the maps, the reader need only see the relationship between various maps to judge similarities and differences.

The following abbreviations are used.

CPM = Coastal Prairie and Marsh Ecoregion
EGCP = East Gulf Coastal Plain
LLP = Longleaf Pine Ecoregion
OPH = Oak-Pine-Hickory Ecoregion
POSa = Post-Oak Savanna Ecoregion
PRA = Prairie Ecoregion
STP = South Texas Plains Ecoregion
WGCP = West Gulf Coastal Plain

We have redrawn all maps from the originals. This has been done to make them interpretable for present purposes. We have taken some liberties to clarify complicated maps. Scholars should consult original maps for detail and original terminology.

In this review—which is done chronologically—we are concerned mainly with geographical areas at and below the ecoregional level. Mapping at higher levels (region, province, subprovince) (Gleason & Cronquist 1964; Good 1974; Cronquist 1982; Takhtajan 1986) is not our concern, although,

since the "provinces" of Dice (1943), Takhtajan (1986), and Gleason and Cronquist (1964) in the WGCP are basically the same as ecoregions, we do discuss them.

Cooper (**1859**; see Stuckey 1978) developed one of the first province maps for North America (Fig. 3). He first described the distribution of tree species in North America and, while performing no statistical analysis, he recognized that different areas had different combinations of species not found in other regions. His map, not dissimilar from that of Takhtajan (1986) and Gleason and Cronquist (1964), was still being reproduced almost a century later (Dayton 1949). He divided North America into provinces and regions. Two provinces interest us: the Appalachian (eastern wooded) and the Campestrian (prairie). We have separated these by a heavy line. He divided each into five regions (we show only four for the Campestrian). The pattern later to be found in many ecoregion and province maps is clearly evident here.

Transeau (**1903**; see also Stuckey & Reese 1981; Delcourt & Delcourt 2000), following in the footsteps of Sargent (1881), produced a simple map of North American vegetation (Fig. 4). His few vegetation types are of interest only in that he included the Cross Timbers and POSa regions in the eastern deciduous forest type and separated the coniferous forest type (what later would become known as the LLP ecoregion).

Harshberger (**1911**) produced perhaps the first widely recognized phytogeographical map of North America, according to which the Atlantic-Gulf Coastal region encompasses most of east Texas and west Louisiana (Fig. 5). To the west of the Atlantic-Gulf Coastal region, Harshberger showed what he called the Ozark area of the Alleghenian-Ozark district, which today would be called the POSa and Cross Timbers ecoregions (POSa on map). Note that the area designated extends well north of Texas. Also note that south and west of this "Ozark area" is a PRA region as well as several other vaguely described regions that extend to the Texas coast. The southernmost, his "Gulf region of the Mexican phytogeographic province," would be our STP. But the others do not follow current usage. The western-most is his "Edwards Plateau forest, meeting ground for species of Atlantic, Rocky Mountain and Mexican forests" (EP on map). The center area is his "Transition Prairie-Forest district, comprising the oak openings" (TRAN on map). This region is a phytogeographic southern disjunct from Wisconsin, Iowa, and Illinois. The final region is his "Texas cross timber and coastal plain belt of heavy live oak with prairies sandwiched between." This today constitutes part of the CPM ecoregion but extends farther inland. Harshberger's use of "cross timber" here is confusing to the modern biogeographer. Also note that the limits of longleaf pine (and many other trees) are shown on his original map but that no longleaf pine ecoregion is recognized. But the salient features of the Harshberger map are that east Texas floristically is firmly joined to the Gulf and Atlantic Coastal plains, and the POSs region is clearly recognized. There are several reprints of Harshberger (1911) but with black and white maps. These are difficult to interpret, and only the colored map of the first edition is satisfactory.

Shreve (**1917**) virtually established the modern WGCP pattern (Fig. 6). He distinguished three WGCP forest regions. The POSa region extends unbroken from south Texas to Michigan, the LLP region extends from southeastern Texas to Florida and North Carolina, and the OPH region extends from Texas to Virginia. This pattern, as will be seen, was followed with very little modification by such influential biogeographers as Braun (1950) and Kuchler (1964). Shreve's original map is in color and cannot be interpreted from black and white reproductions of which there are many.

Shantz and Zon (**1924**), in their widely reproduced map, added essentially nothing to Shreve (Fig. 7). The Shantz and Zon map has been widely reprinted, sometimes with minor modifications (Fenneman 1938; Barrett 1962; Fowells 1965).

Tharp's (**1926**) interest was regional (Fig. 8). He mapped Texas east of the 98th Meridian and did extensive field work throughout east Texas. He provided extensive descriptions of the vegetation regions. His captionless map (his plate III) is confusing, and the text requires careful study for complete interpretation. But his map is the basic pattern that is familiar today: a LLP region in southeast Texas, a coastal region, an OPH region to the north and west of the LLP region, and a

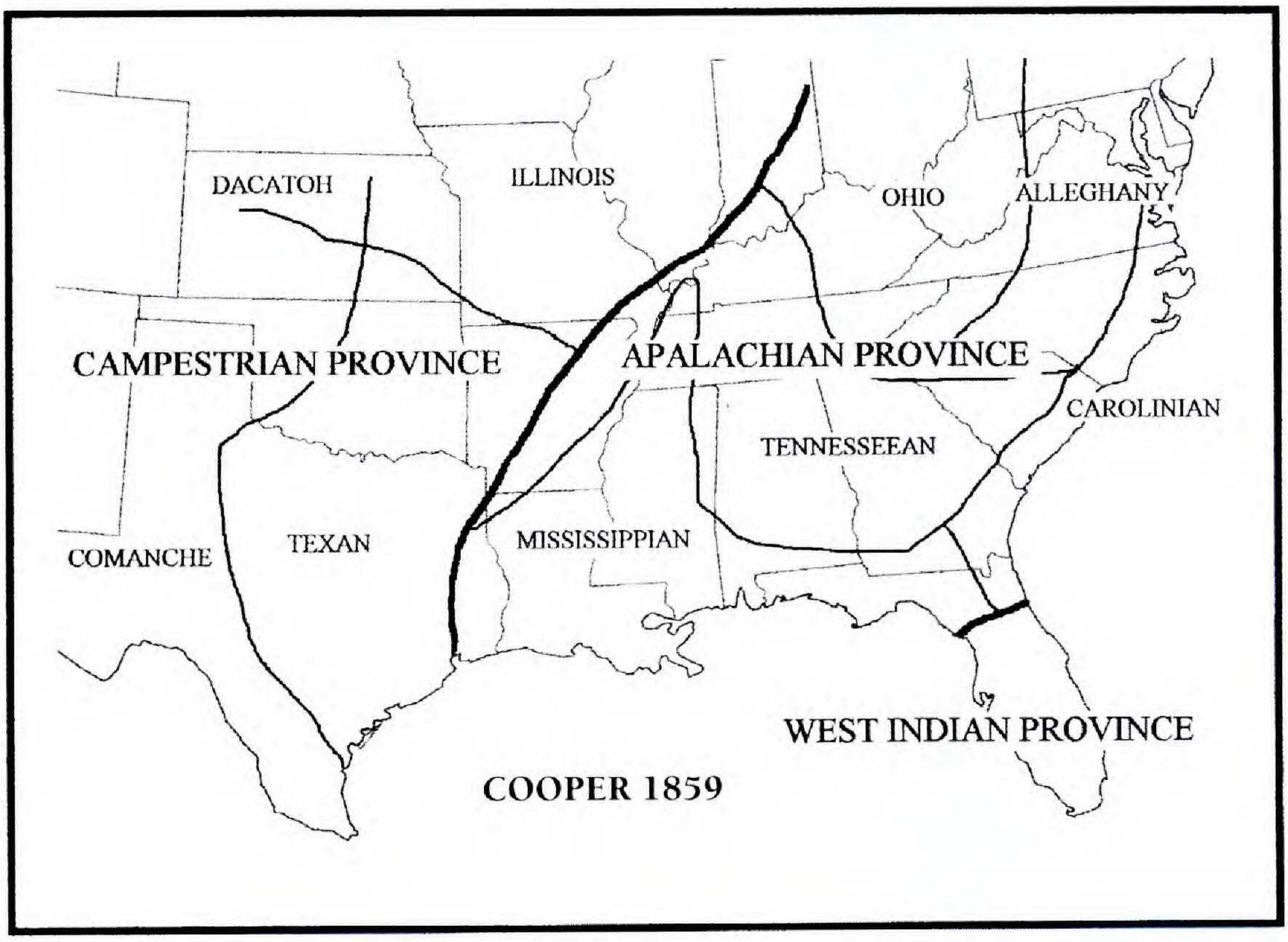

FIG. 3. Vegetation areas according to Cooper (1859).

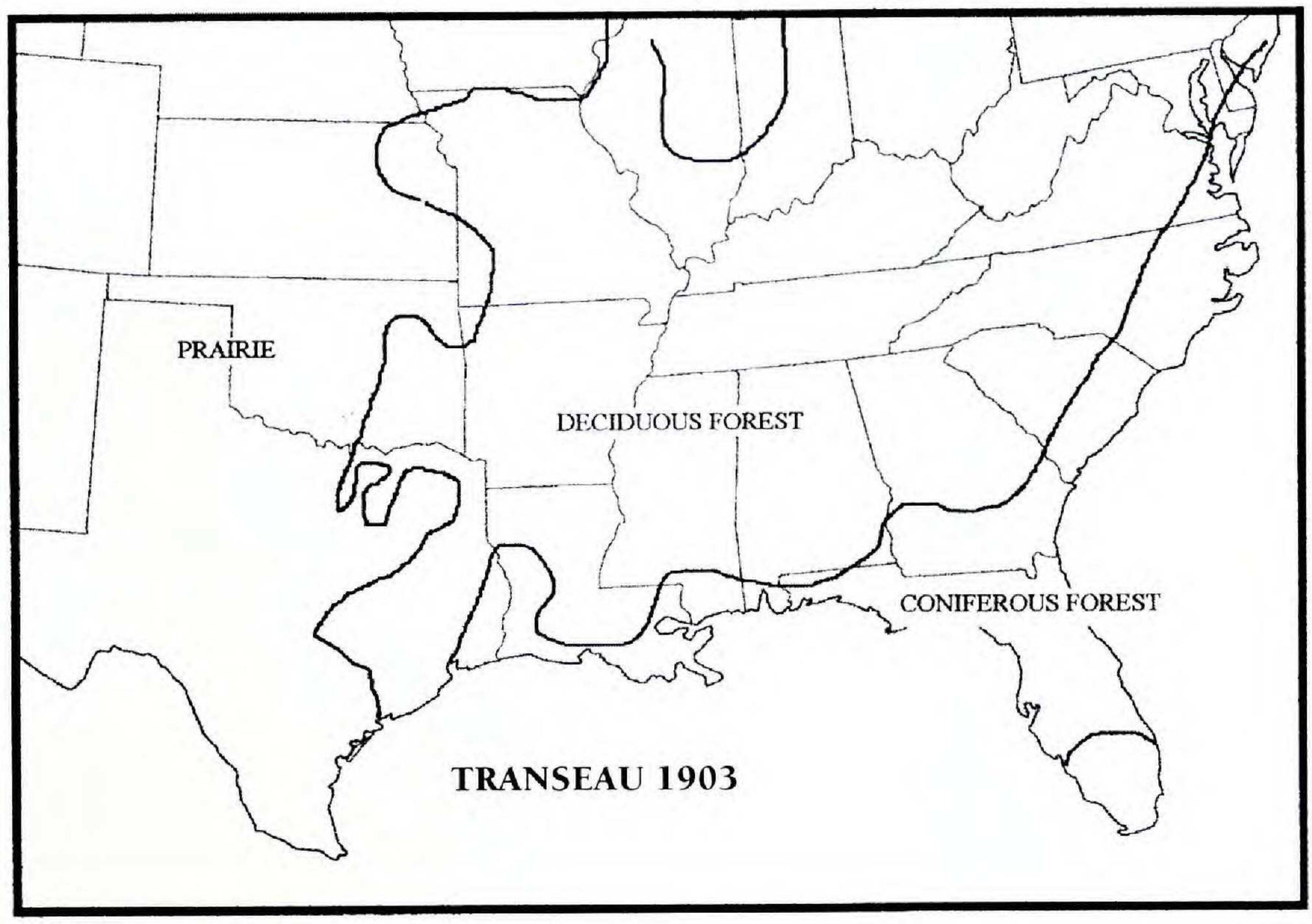

FIG. 4. Vegetation areas according to Transeau (1903).

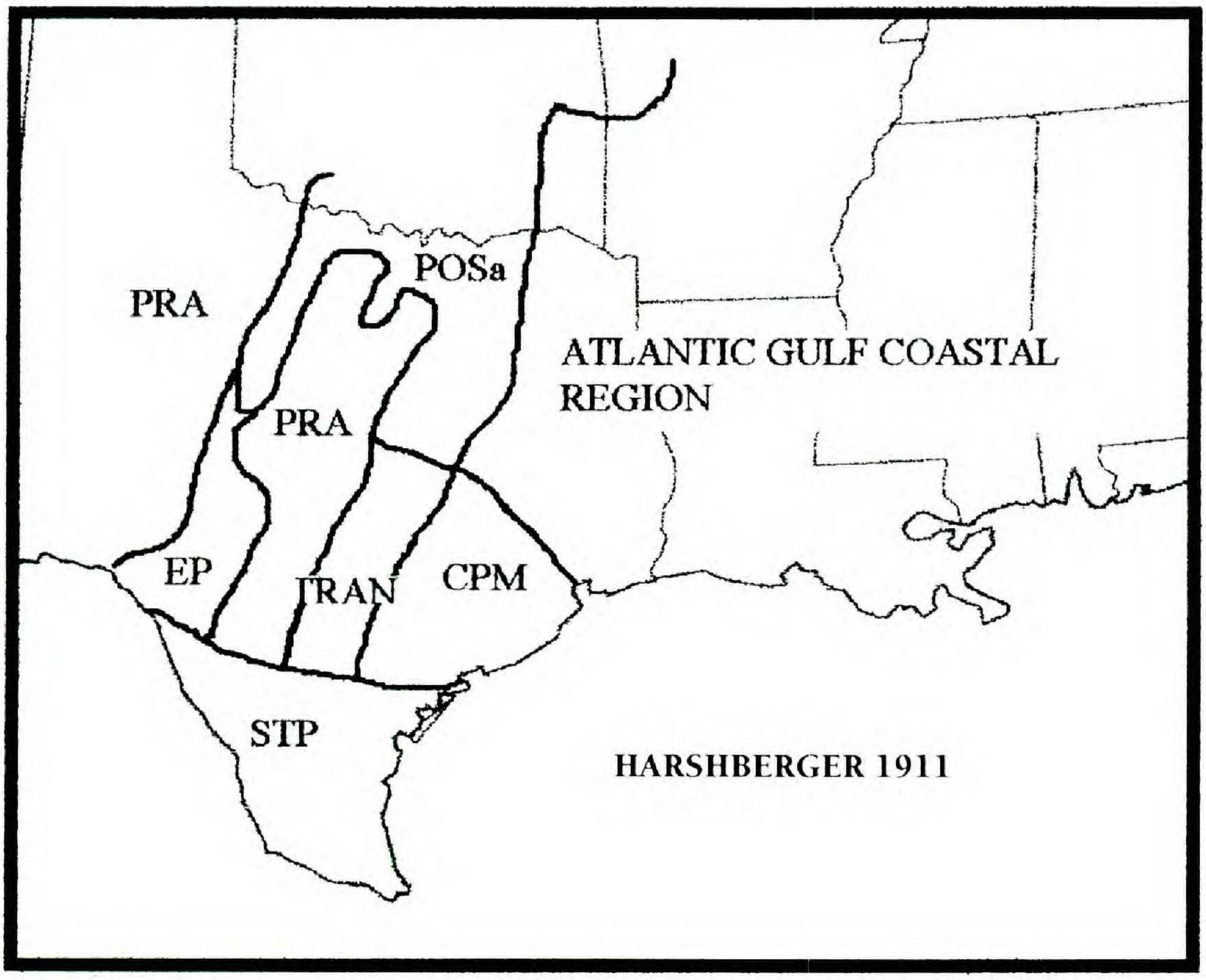

Fig. 5. Vegetation areas according to Harshberger (1911).

POSa region to the west of the OPH region. Tharp divided the POSa region into two areas. To the north, prairies are not common but to the south is an "oak-prairie mictium," that is, a combination of POSa and prairie southwest of the Brazos River. Later biogeographers showed this area as POSa with islands of prairie in it (e.g., Gould 1962; Diamond & Smeins 1988).

Carter (1931), the chief soil scientist for the Texas Agricultural Experiment Station, in his survey of the soils of Texas, produced a vegetation map for the whole state (Fig. 9). The accompanying soil map, while not matching the vegetation patterns precisely, does delineate the distribution of "main areas of deep sands" that correspond closely with the POSa region. Descriptions of the regions are given in his text.

Fenneman (1938) produced a slightly modified Shantz and Zon (1924) map (not reproduced here). He filled in the non-forested areas along the coast of Louisiana and Texas that they left blank. A modified version of this map is in Bonnicksen (2000).

Tharp (1939) refined his regional vegetational map (Fig. 10). In this version, the lines that were tentative in 1926 are bold. The WGCP is virtually identical to that given by Carter (1931), and any comparison of Tharp's map to that of Gould twenty years later leaves no doubt about influences. Tharp's brief descriptions of the vegetational regions are often folksy but never dull. Tharp's map was used by Wynd (1944).

Dice's (1943, 1968) "biotic provinces" are at a descriptive level above the ecoregion (Fig. 11). In this scheme, Dice divided east Texas into two regions: the Austroriparian and the Texan. The Austroriparian encompasses basically the entire Atlantic and Gulf Coastal Plain (OPH and LLP). The

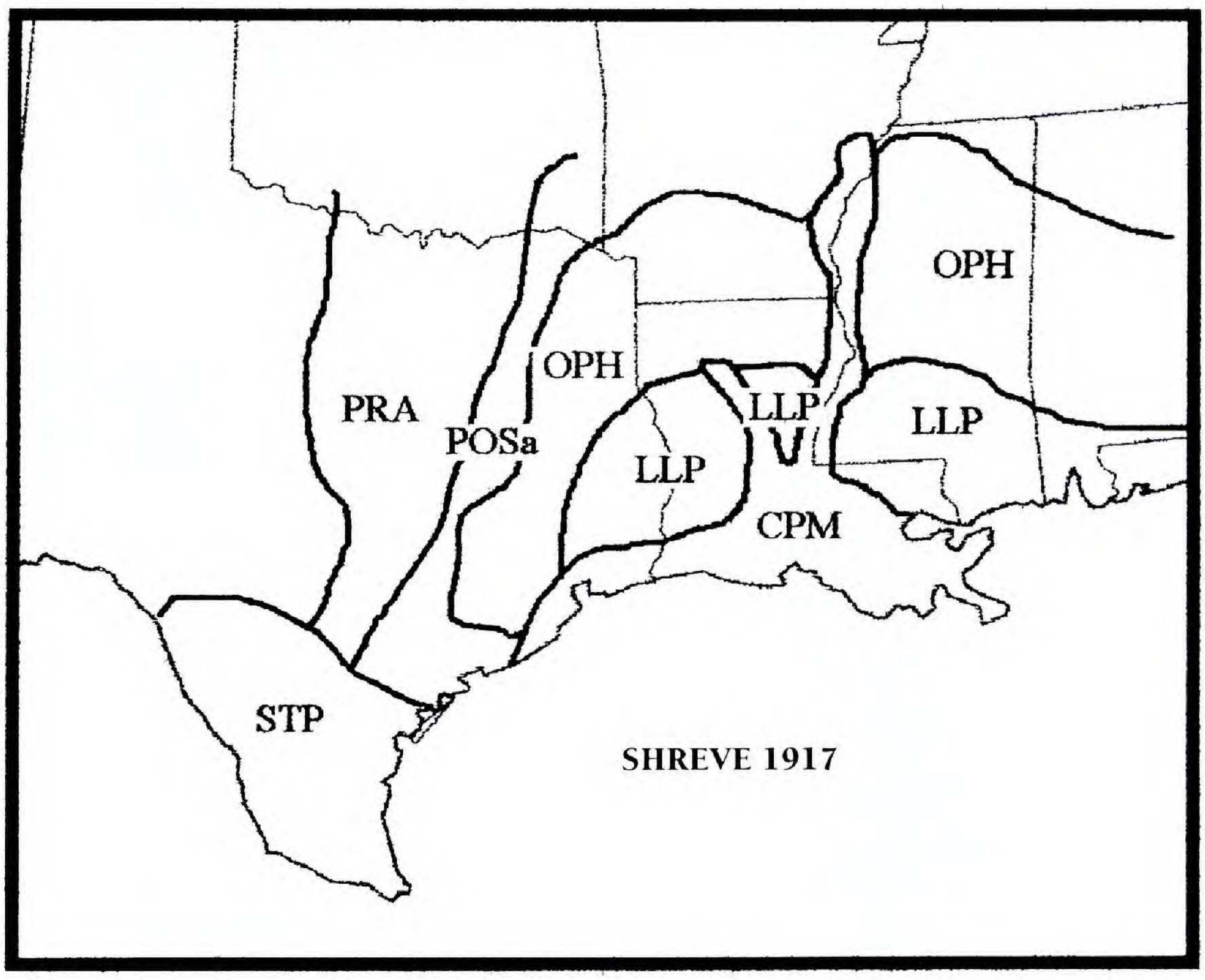

Fig. 6. Vegetation areas according to Shreve (1917).

Texan takes in the POSa as well as the prairies and cross timbers regions, and extends from central coastal Texas to northern Oklahoma. Blair (1950) followed Dice in his description of the east Texas biotic provinces but added nothing.

Braun's (1950) classic work on eastern forests adds little to our knowledge of the WGCP region (Fig. 12). Her map of "Forest Regions" is essentially identical to that of Shantz and Zon (1924) with only minor boundary shifts. She kept the three "regions" format: LLP, OPH, and POSa. While Braun sampled vegetation widely across the east, and produced tables of percent composition from many sites, but none from the WGCP, she did not statistically compare regions, but left that to her successors (e.g., Delcourt & Delcourt 2000).

Tharp's (1952) final map (not reproduced here) of the vegetation regions represents revisions and refinements of maps in his 1926 and 1939 publications. The greater detail is based on a decade of additional field experience, but the refinements for the WGCP are relatively minor and add little to his earlier work. Consequently, we do not present a separate map; however, it should be noted that his brief descriptions of each vegetation region are succinct and clear.

Turner (1959) is unique among WGCP authors in that he used quantitative methods to determine what he calls "floral provinces" (Fig. 2). We have discussed his work in the first part of this paper.

Gould's (1962) map is clearly influenced by Carter's (1931) and Tharp's (1926, 1939, 1952) work (Fig. 13). The map and slight variants have been used extensively (e.g., Correll & Johnston 1970; McMahan et al. 1984; Hatch et al. 1990; Diggs et al. 1999) and one version of it presents subregions (e.g. LBJ School of Public Relations 1978; Diamond et al. 1987; Telfair 1999).

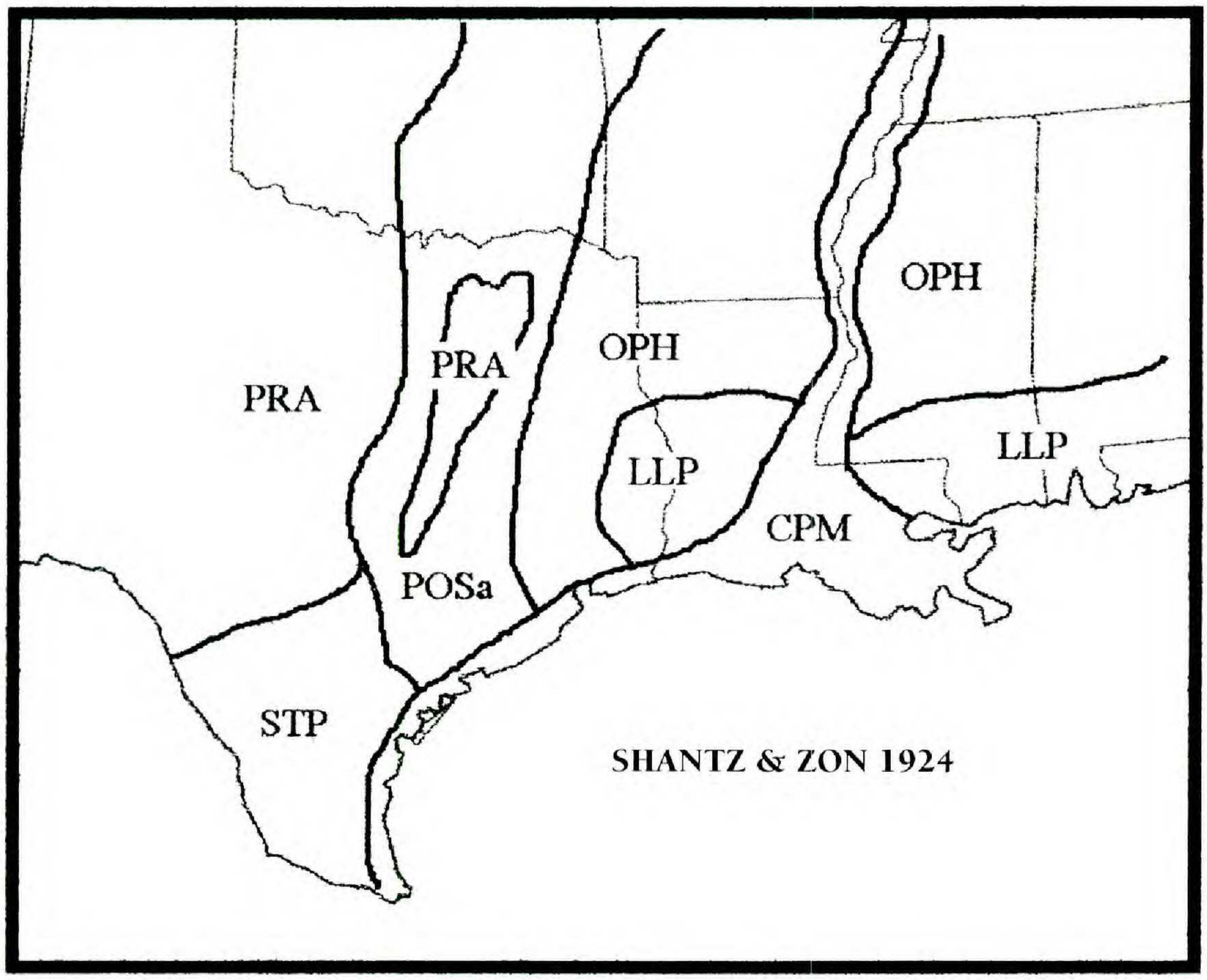

Fig. 7. Vegetation areas according to Shantz and Zon (1924).

Gleason and Cronquist (1964) detailed ten floristic provinces of North America, four of which occur in the WGCP (Fig. 14). What is of interest to us in this map is the association of the POSa region, notably regions as far south as Guadalupe County in Texas, with regions as far north as Maine, southern Ontario, Michigan, and Minnesota: this entire area Gleason and Cronquist called the Eastern Deciduous Forest Province. The floristic similarity among extreme parts of this large region is very small indeed. At the same time, their Coastal Plain Province is nothing more than the traditional Atlantic and Gulf Coastal Plain that extends from east Texas to Florida and north to Virginia—a much more floristically homogeneous region than the Eastern Deciduous Forest Province. Takhtajan (1986) produced a province map of North America virtually identical to that of Gleason and Cronquist (1964), which has been reproduced (Thorne 1993) (Fig. 15).

Kuchler's (1964) map, "Potential Natural Vegetation of the Conterminous United States," has become the "central dogma" of North American biogeographers upon which all other maps are judged (Fig. 16). It is widely cited and used (e.g., Martin et al. 1993). The Kuchler map presents no novelties for the WGCP; it is virtually identical with those of Shantz and Zon (1924) and Braun (1950).

Mahler (1981) presented an interesting variation on the Gould (1962) map (Fig. 17). Apparently following the lead of McLeod (1971), he designated not a LLP ecoregion in southeast Texas but a Beech-Magnolia-Pine-Oak-Sweet Gum (Big Thicket) region overlying most of the traditional LLP ecoregion. Why Mahler (1981) chose this course is not clear, but it underlines the fact that other ecoregion descriptions can be considered.

Omernik's (1986) was the first ecoregion map where ecoregions no longer straddle the Mississippi River (Fig. 18). Additionally, Omernik did not divide the pineywoods region into two

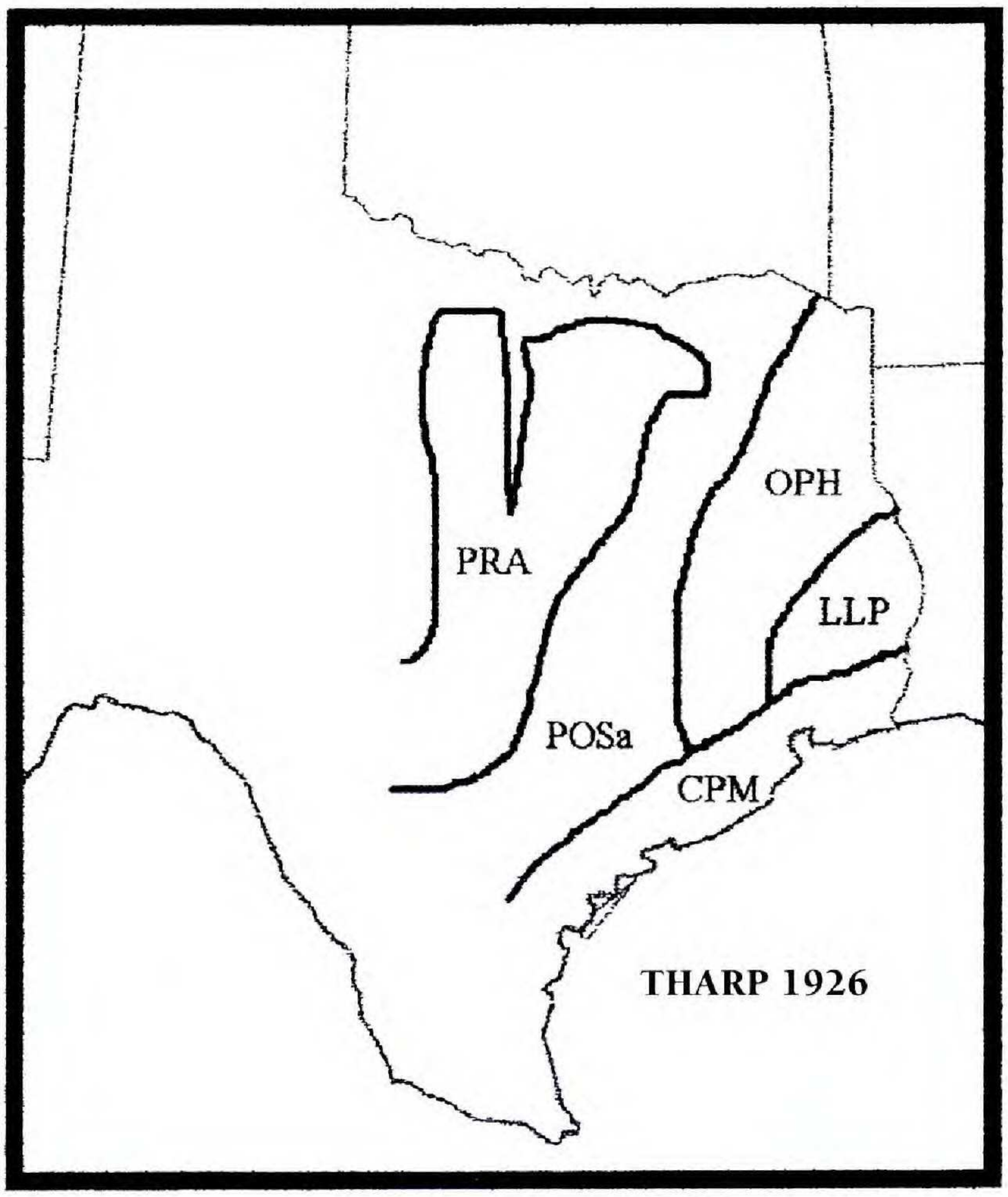

Fig. 8. Vegetation areas according to Tharp (1926).

ecoregions (OPH and LLP) but like Gould (1962) kept them together. Otherwise, the familiar pattern is maintained. But what is interesting here is that the LLP region is not uniquely distinguished in either the WGCP or EGCP. How Omernik distinguished EGCP ecoregions from WGCP ecoregions is not evident since his brief descriptions are virtually of no help.

Greller (1988) produced a map that he claims is based on Braun (1950) but which shows no closer relation to hers than it does to the maps of Shantz and Zon (1924) or Kuchler (1964) (Fig. 19). What is unique about Greller's map is that it combines the POSa and the OPH regions with no explanation given (but see Turner 1959). Greller did, however, retain the other traditional ecoregion features, such as the LLP ecoregion.

Barbour and Christensen (1993) presented a relatively simplified vegetational map of North America (Fig. 20). We find in it the traditional LLP and OPH regions, but the POSa region has been separated and joined into a vast region stretching from the Gulf of Mexico to Canada. This region is described as "tallgrass prairie, including the prairie peninsula and oak savanna ecotone with the eastern deciduous forest" (1993:98). Treating the POSa region as an "ecotone" and including it in the prairie ecoregion has been commented on (Gehlbach 1991) and is reminiscent of Dice's (1943, 1968) and Blair's (1950) "Texan" biotic province.

Bailey et al. (1980, 1994, see also DeGraaf et al. 1988; McNab & Avers 1994) resurrected the old Texan biotic province of Dice (1942, 1968) and Blair (1950), and then divided it into four subregions (Fig. 21). This ecoregion ("province" and "ecoregion" are apparently synonyms here) extends

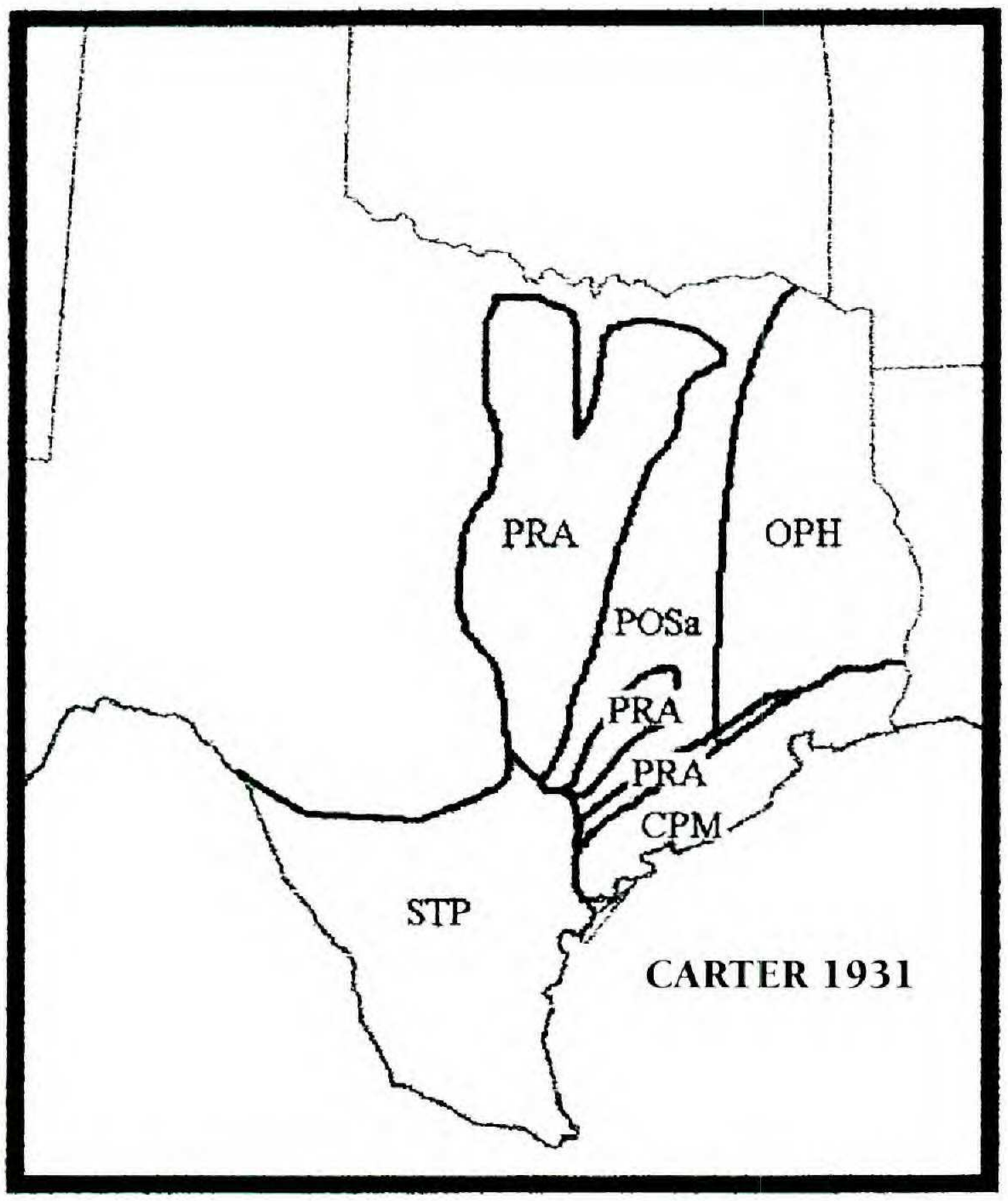

Fig. 9. Vegetation areas according to Carter (1931).

from the Texas coast to northern Oklahoma. The eastern most part is separated as the "Oak woods and prairies subregion" (255C), which is virtually identical to the POSa region of previous writers except that it includes several major sections of the prairie region of east Texas, such as Fayette Prairie. This makes the Bailey "Oak woods and prairies subregion" non-comparable with the maps of most other biogeographers. Like many before them Bailey et al. (1994) divided the remainder of the WGCP in two regions. The southern one corresponds with the LLP, and the northern one corresponds to OPH. At the subregional level, however, they separated both the OPH and the LLP regions west of the Mississippi River from the OPH and LLP regions east of the Mississippi River. What distinguishes these areas, aside from geographical location, is not disclosed, and the McNab and Avers (1994) descriptions do not help. It should be further noted that the Bailey (1994) text and the McNab and Avers (1994) descriptive material are peppered with factual mistakes, something not found in previous biogeographic descriptions.

The map of **Keys et al. (1995)** and **Bailey (1994)** are virtually identical. Because the Key et al. (1995) map is more detailed, the western boundary of the WGCP is more easily distinguished (Fig. 22). The northern POSa region may have been included in the OPH region while the southern POSa may have been included with the Prairies sections. Bailey et al. (1994) may have done this also, but that map is cruder and harder to decipher: they may have put the entire POSa region in with the prairie group. The Keys et al. (1995) map divides ecoregions into dozens of "nested" subsections that are not readily distinguishable on the basis of their descriptions (nor are they distinguished by regional ecologists and botanists). Also, the Keys et al. (1995) map is clearly based on a poor knowledge of the WGCP. The text presents several factual mistakes.

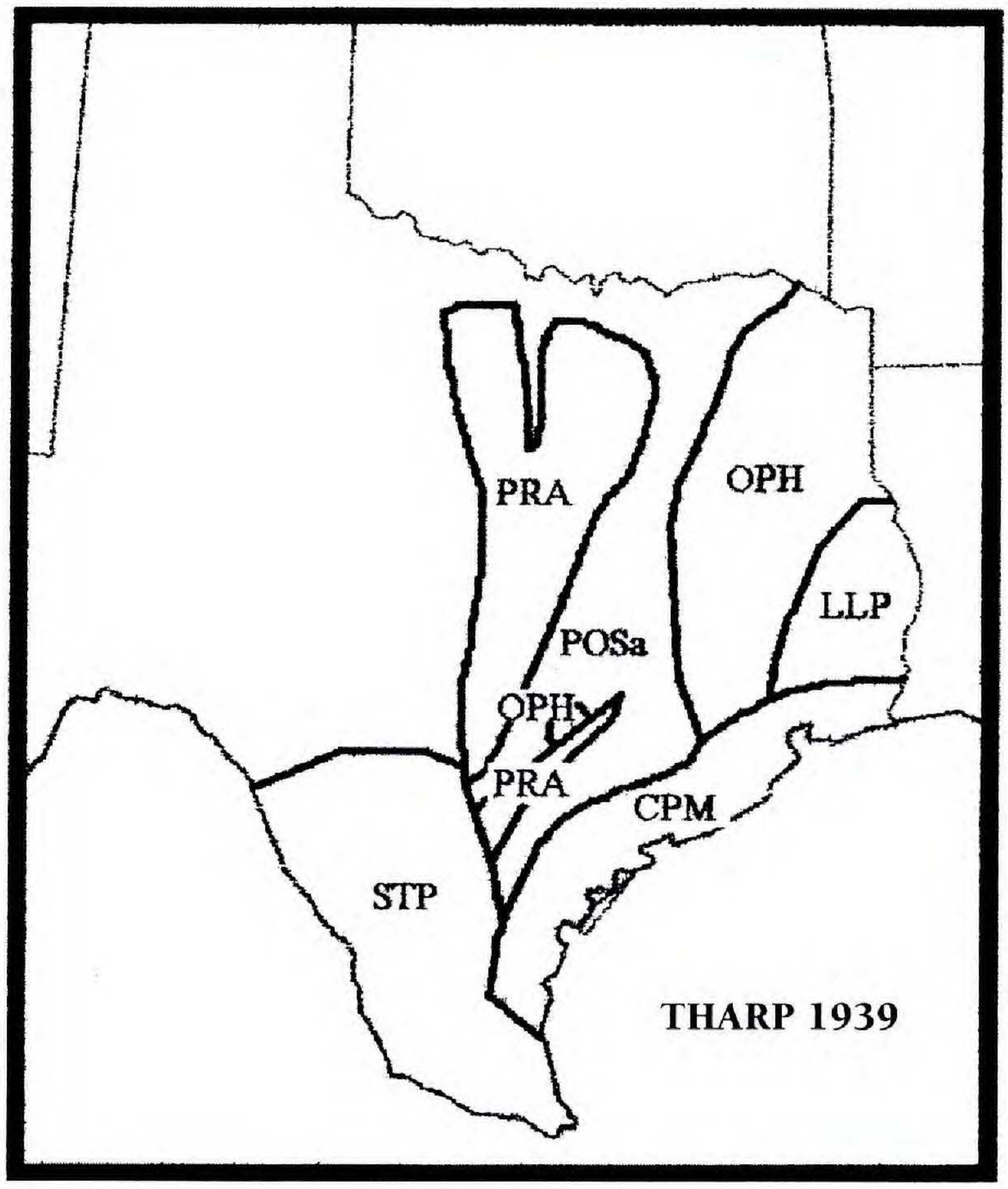

Fig. 10. Vegetation areas according to Tharp (1939).

The Nature Conservancy (**Weakley et al. 1998**; Turner et al. 1999) relies heavily on Keys et al.(1995) and Bailey et al. (1994), and it is through the Nature Conservancy maps that it is possible to detail precisely where the Keys et al. (1995) ecoregions, provinces, sections, and subsections are (Fig. 23). The POSa region has disappeared as a region. In the north, it is divided between the prairies region and the "Upper West Gulf Plain" region. In the south, the "West Gulf Coastal Plain" region is basically coterminous with Longleaf pine. This new terminology should lead to confusion.

Ricketts et al. (**1999a, 1999b**) divided North America into two phytogeographic levels. The first is ten Major Habitat Types in which most of the WGCP is lumped with the LLP region and not with the OPH region of the east, and the POSa region is lumped with the majority of the east but is geographically separated from it. At the finer level, in the WGCP the traditional LLP and OPH regions are lumped into the "pineywoods region;" whereas in the EGCP, they are inexplicably kept separate. The POSa region is separated from the "pineywoods." In the EGCP, while the traditional LLP and OPH regions are recognized, they are ignored in the WGCP. The descriptive sections of this account are replete with factual mistakes, and it is clear that part of the problem is a heavy reliance on Bailey et al. (1994). Ricketts et al. (1999a, 1999b) apparently believe that longleaf pine occurs over the entire "pineywoods" region. Since the Ricketts et al. maps of the WGCP are identical with Omernik's map, the reader is referred to that map for detail.

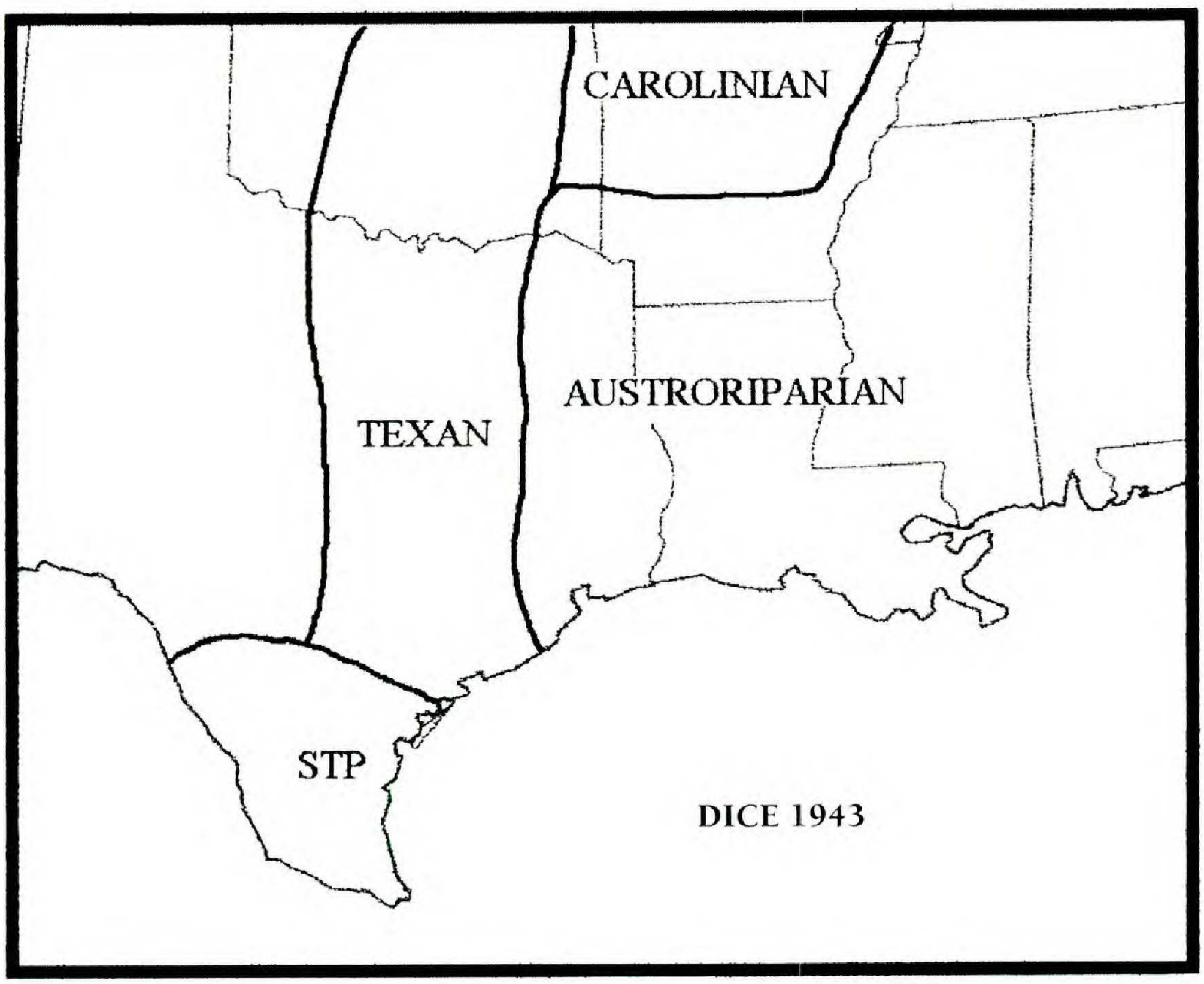

FIG. 11. Vegetation areas according to Dice 1943, 1968).

CONCLUSIONS

In summary, there has been relatively little evolution of the "ecoregion" maps of the WGCP over the 20th century. The patterns, but not the precise boundaries, found in the earliest maps are found in the later ones. The main questions appear to be whether or not to join the WGCP with the EGCP, whether or not to join the LLP region with the OPH region, and what to do with the POSa region? Should the latter be a part of a mega-region stretching from south Texas to Michigan? Should it be combined with the prairie region to the west, should it be kept separate from all other regions, or should it be cut in half and part of it put with the prairies and part with the OPH region? About half of the mappers recognize an LLP ecoregion, while the rest do not. It would appear that botanists who have constructed floras or distribution maps do not recognize a separate LLP ecoregion, presumably because the vegetational distinctiveness is either minor or virtually nonexistent (Correll & Johnston 1970; Gould 1975; Vines 1977; Nixon 1985; Hatch et al. 1990; Nixon & Kell 1993). Turner (1959) is the prime example of this. It is mainly ecologists who distinguish a separate LLP region.

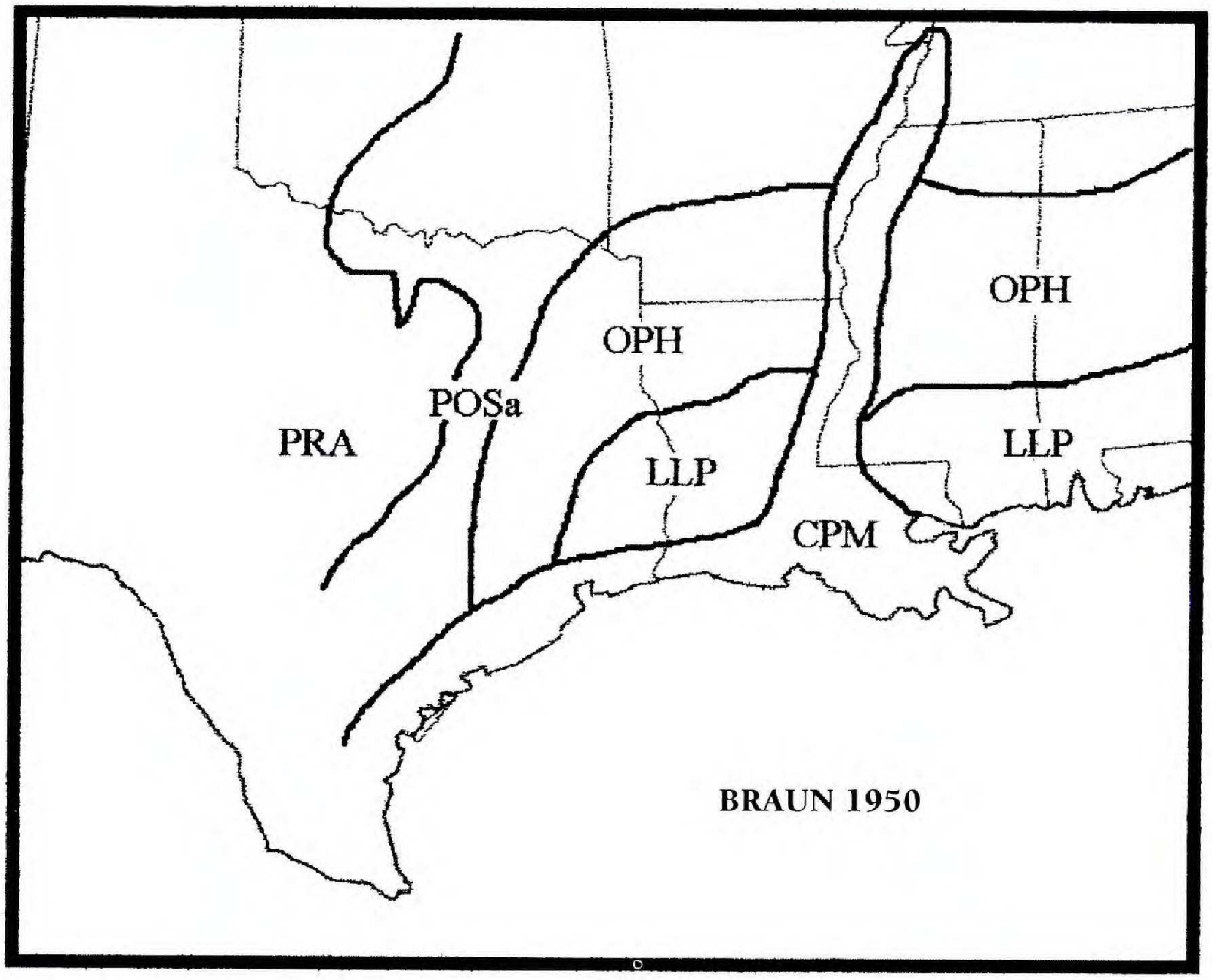

Fig. 12. Vegetation areas according to Braun (1950).

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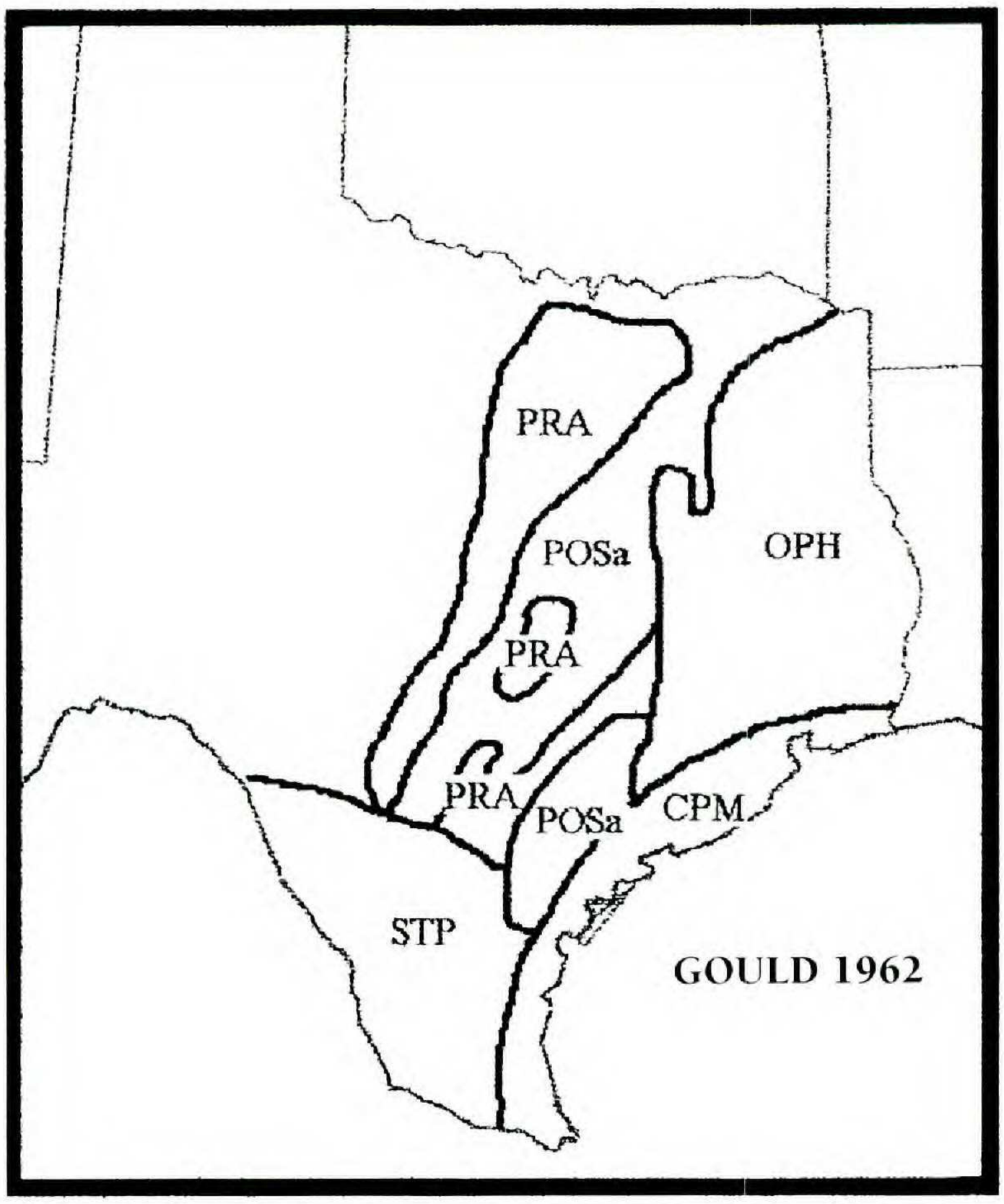

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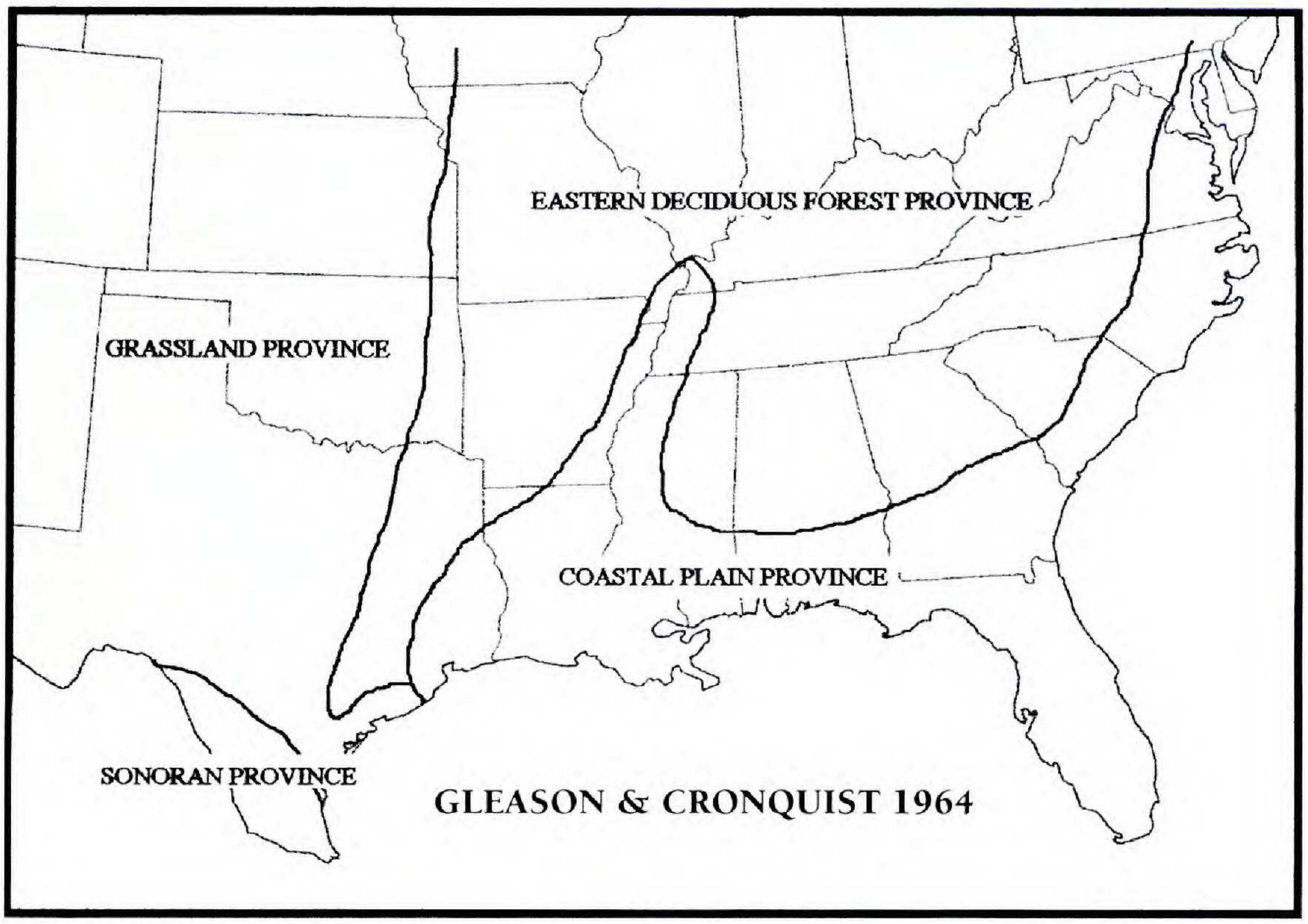

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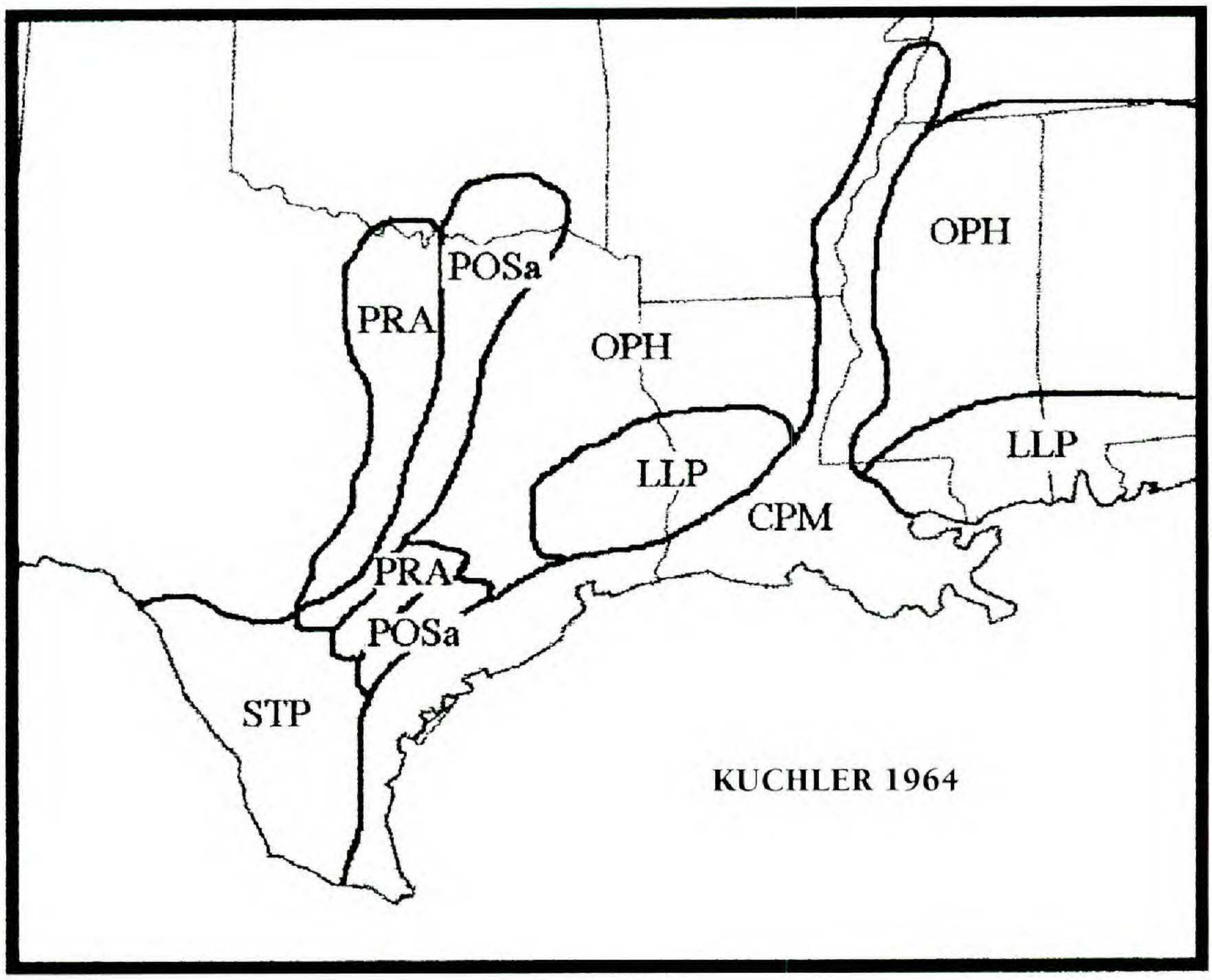

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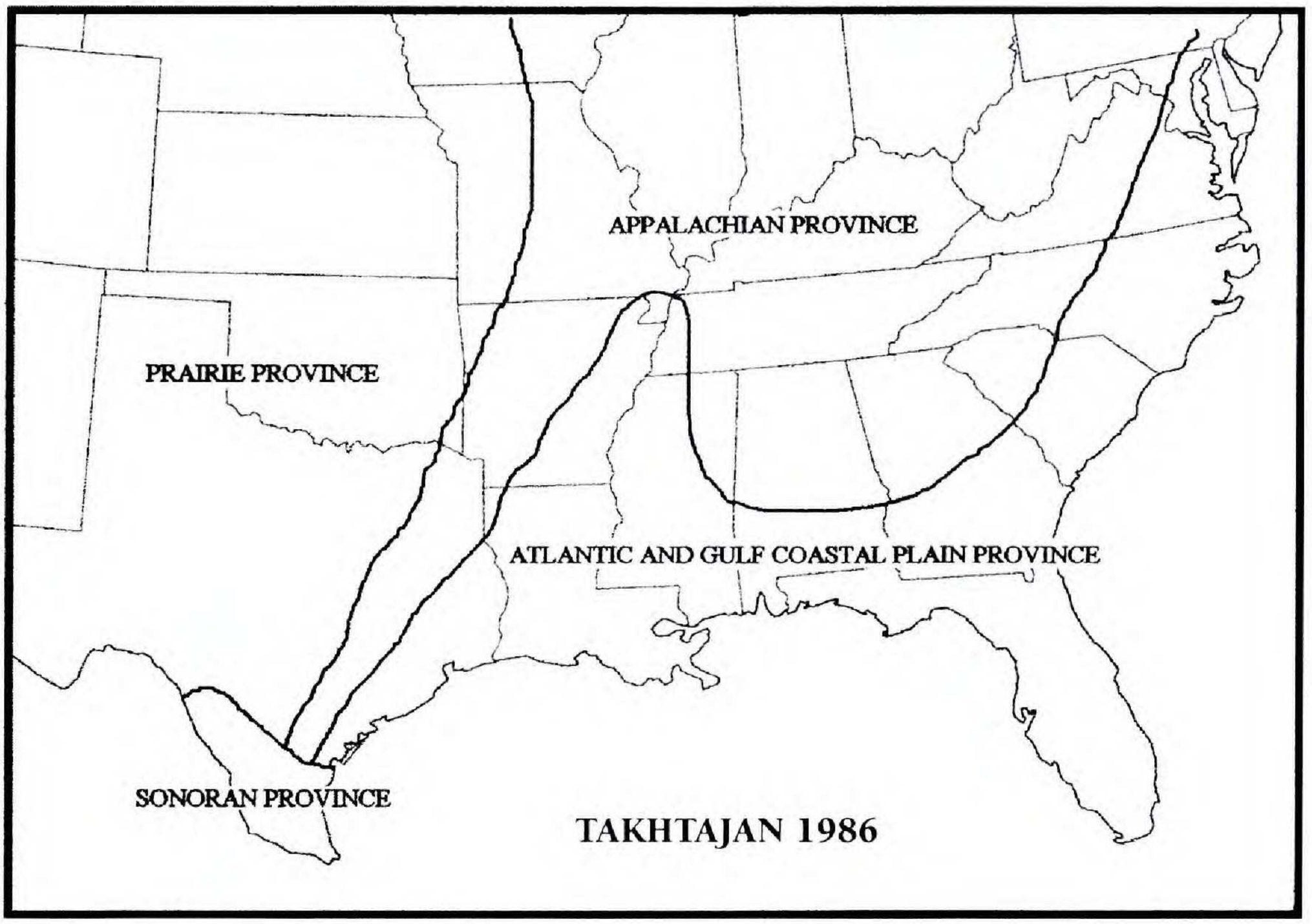

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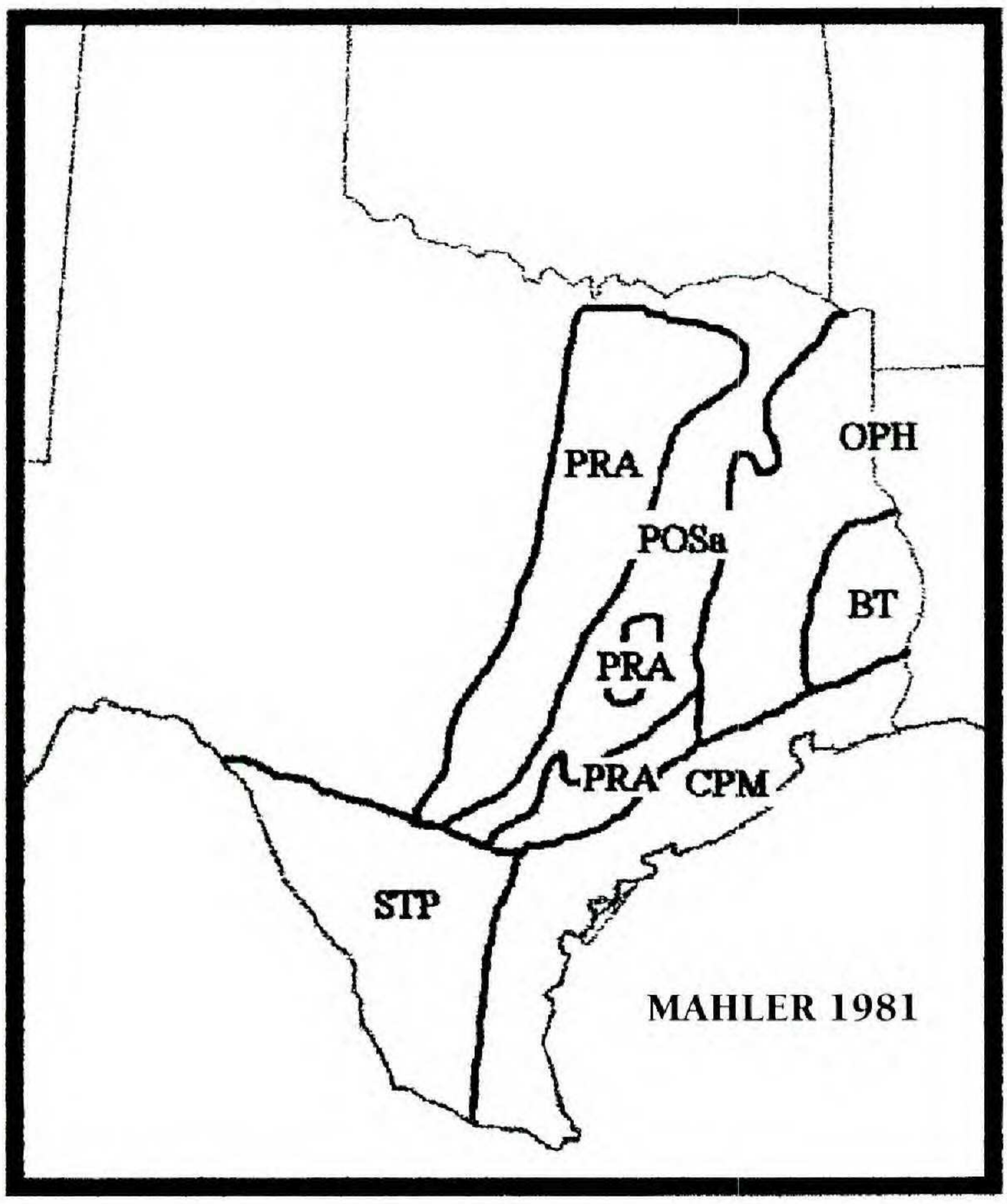

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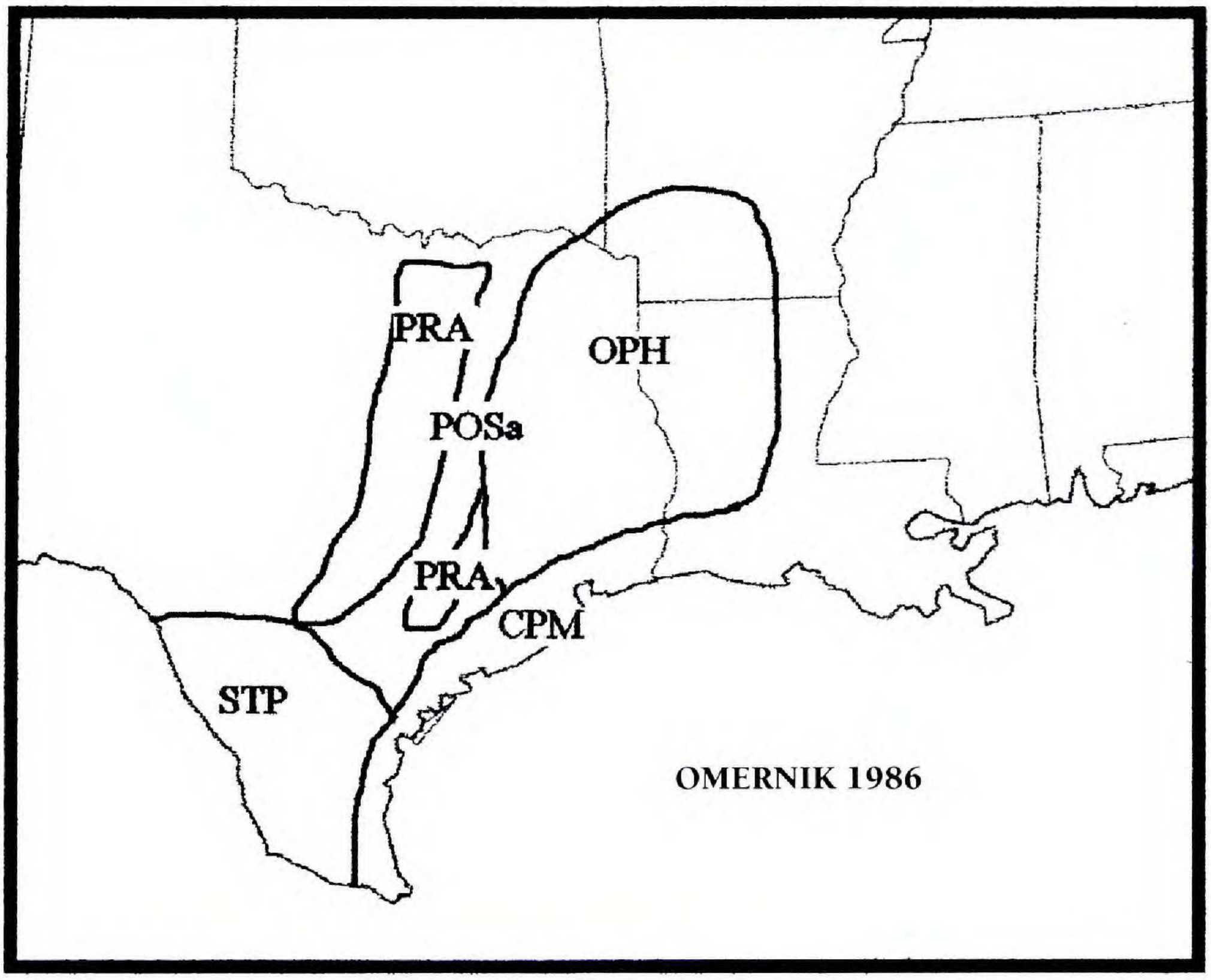

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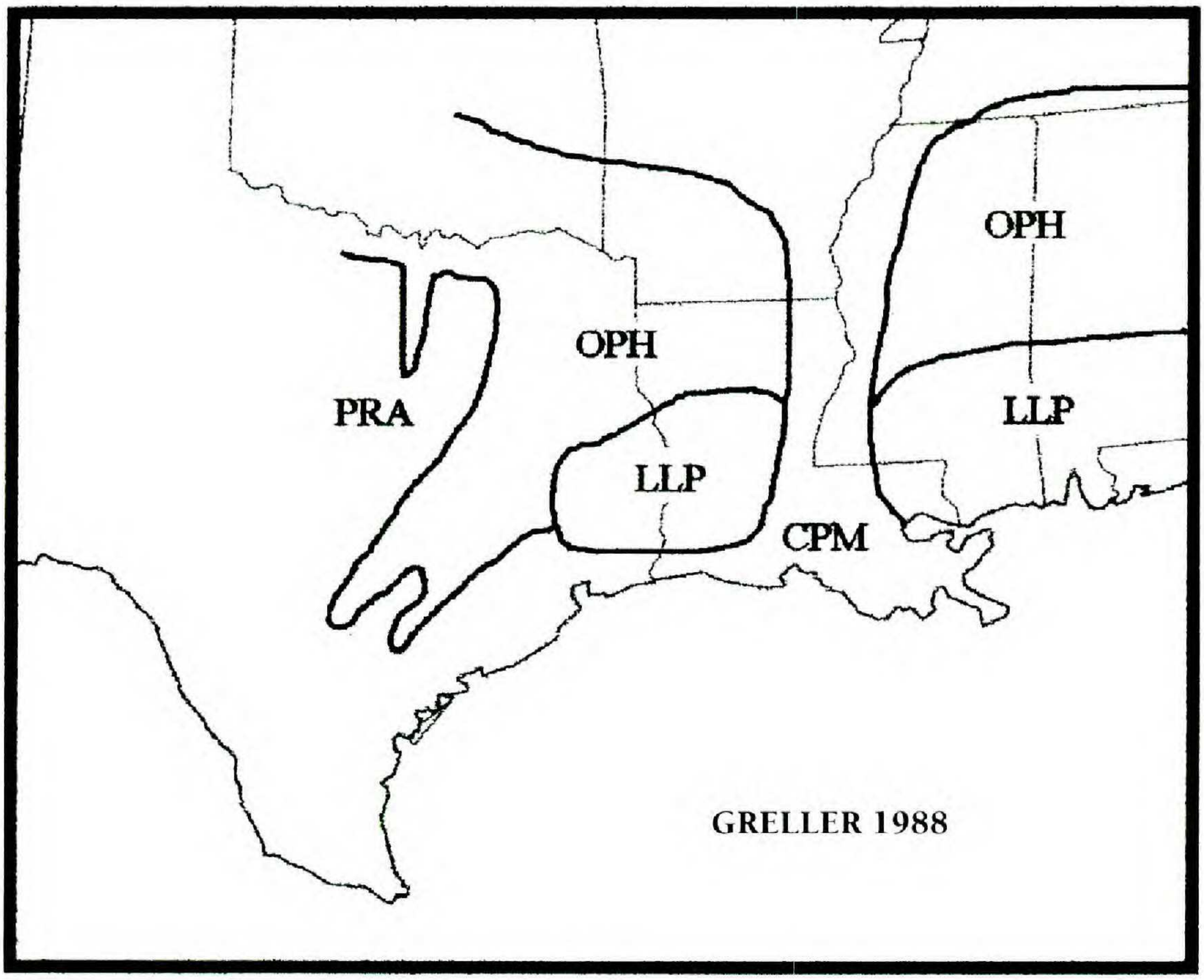

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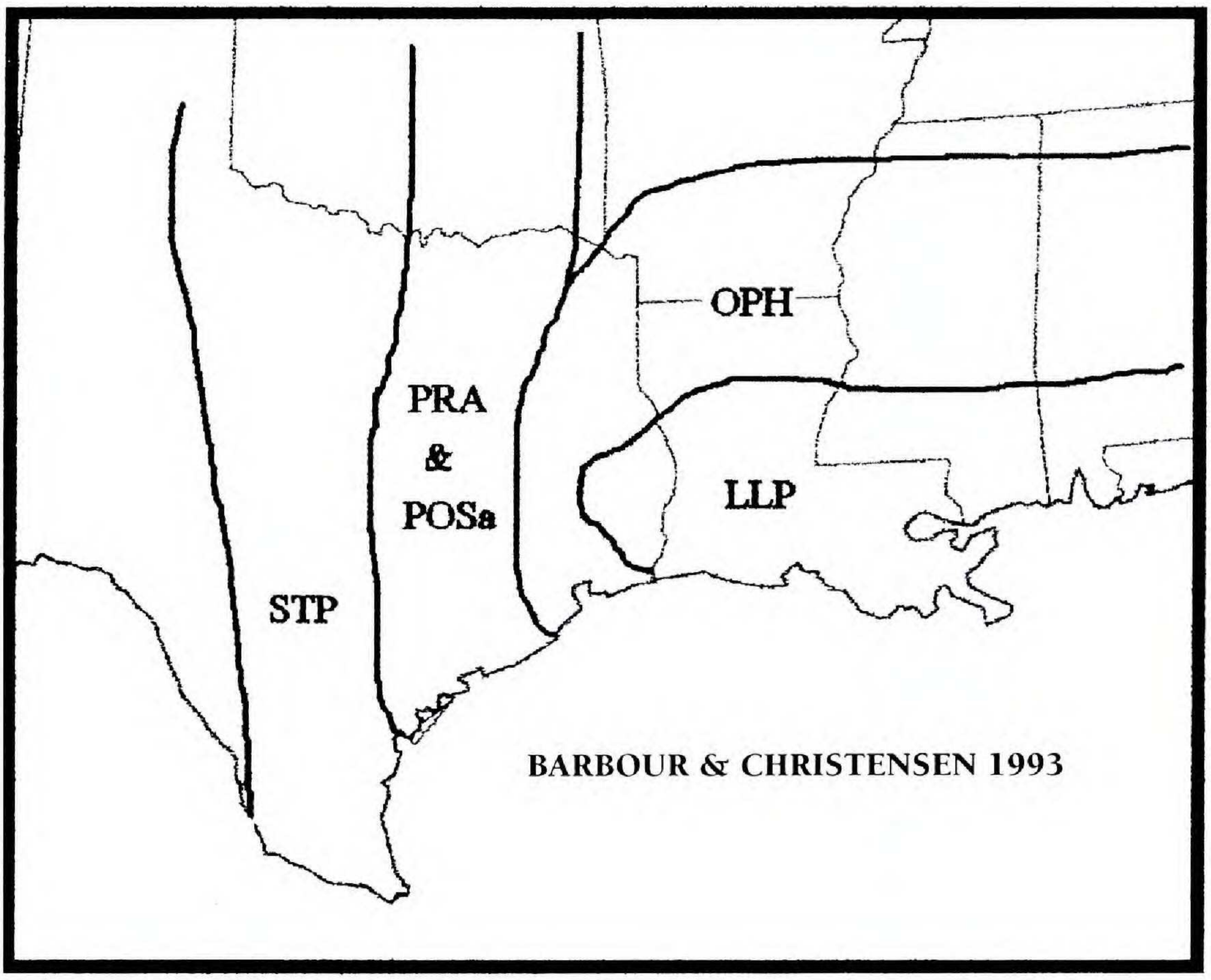

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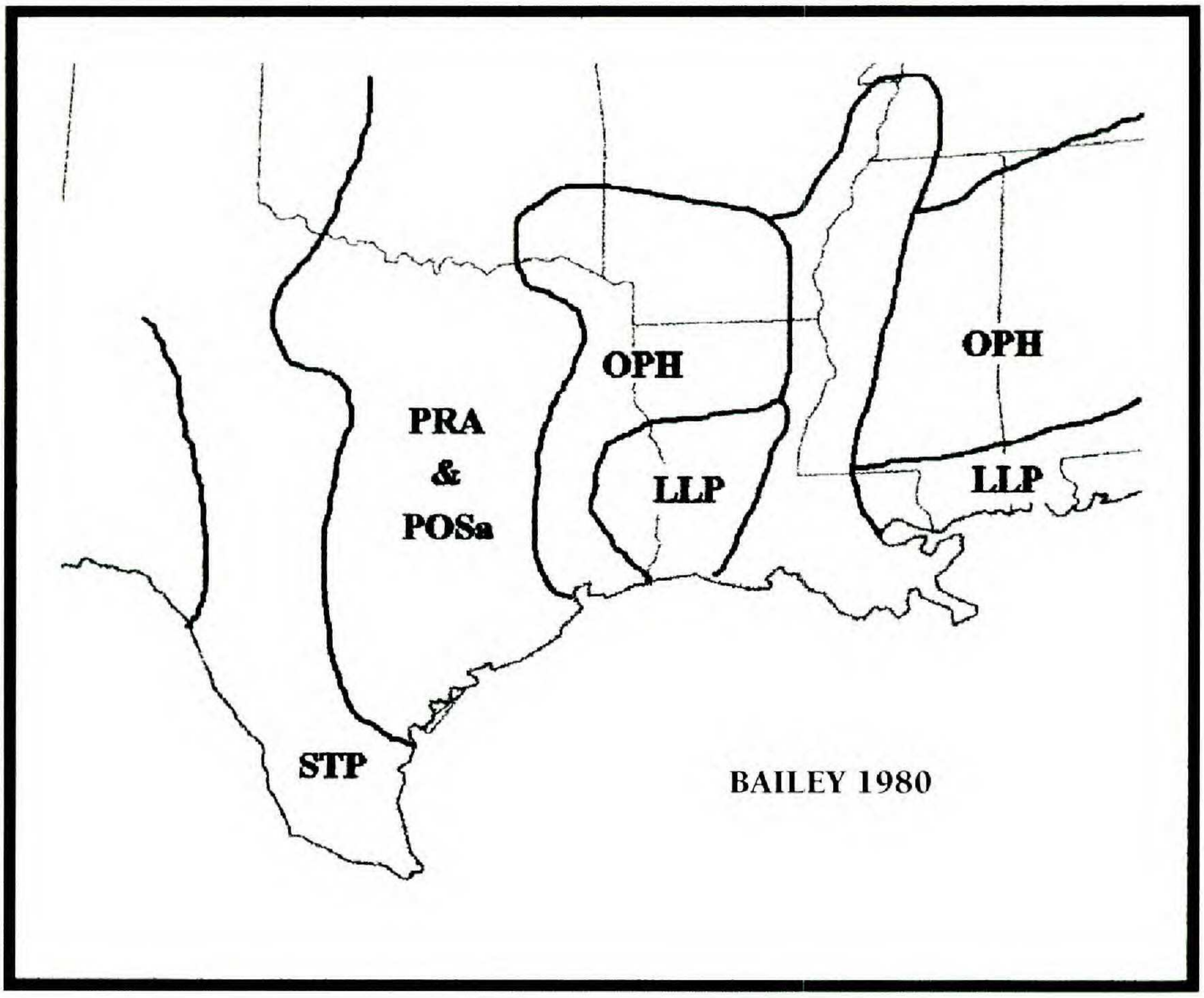

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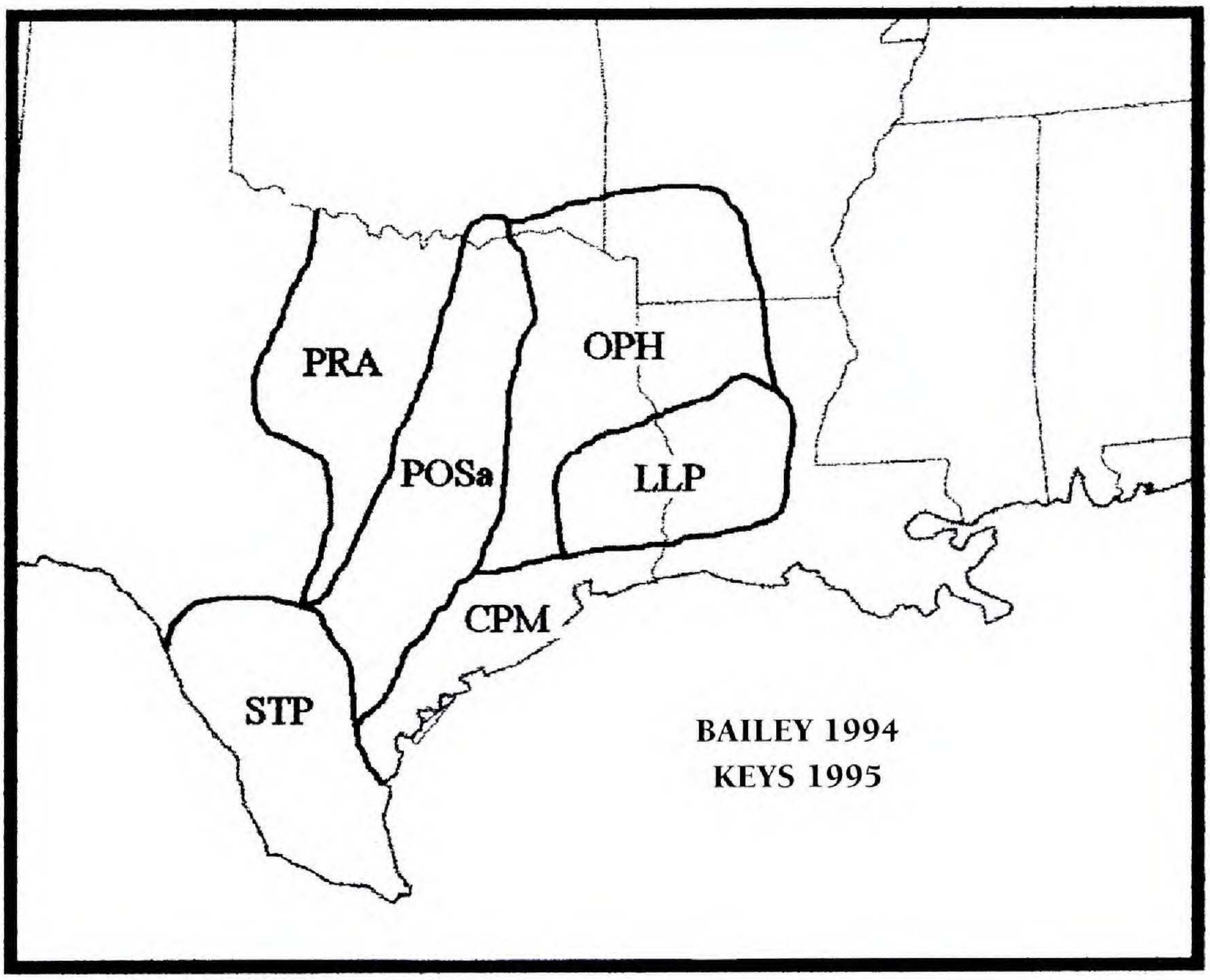

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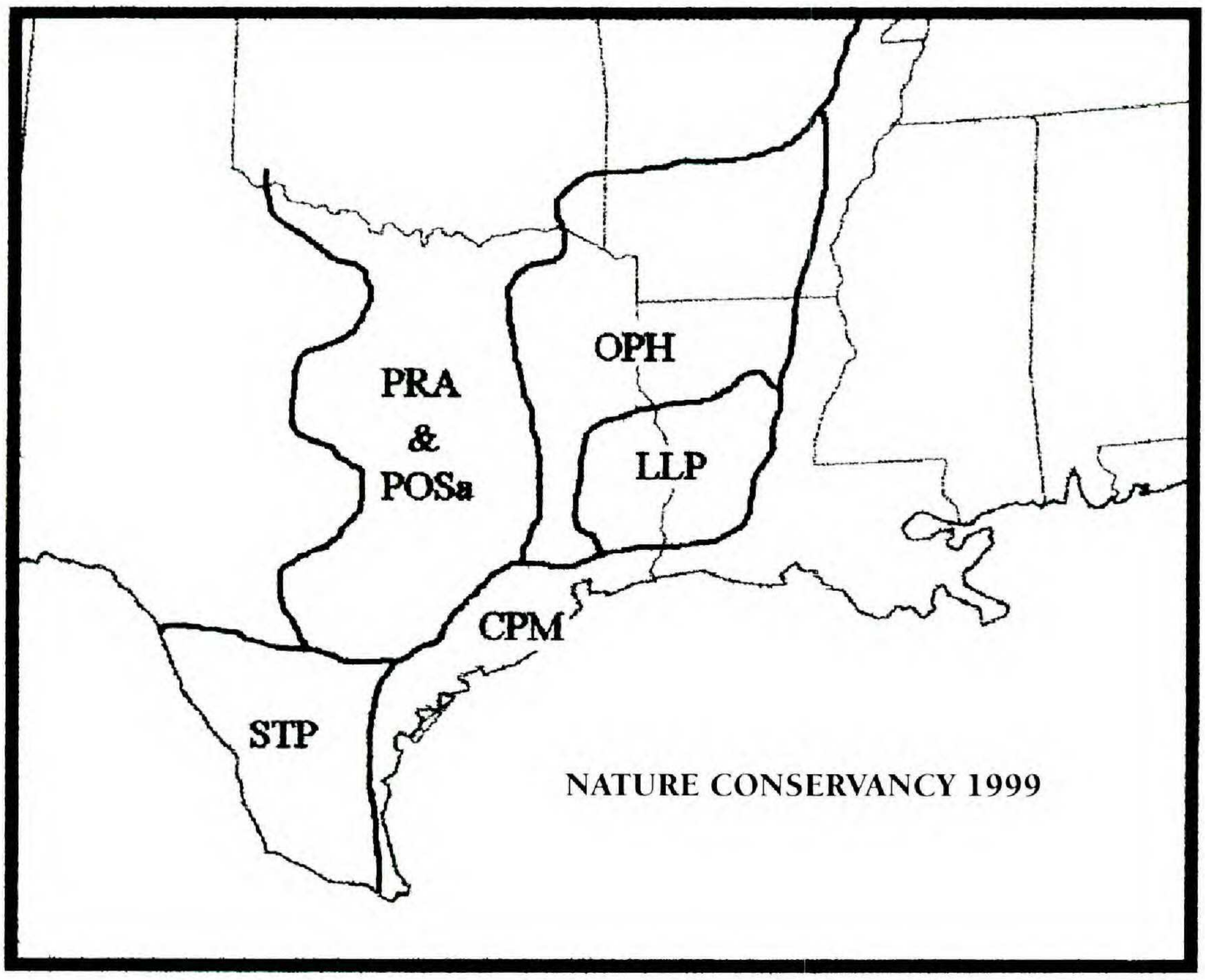

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